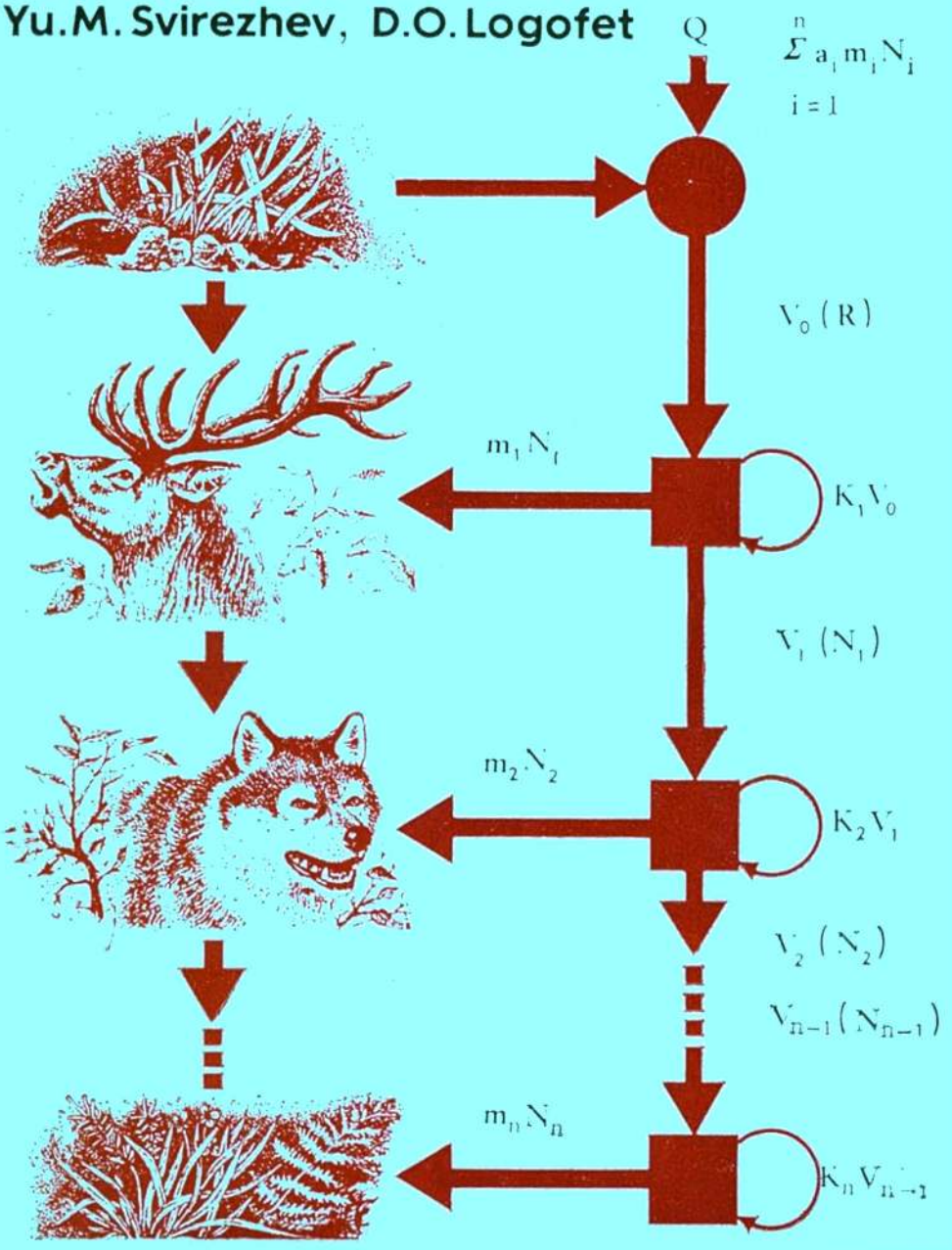
STABILITY OF BIOLOGICAL COMMUNITIES

Yu. M. Svirezhev, D. O. Logofet



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Ю. М. СВИРЕЖЕВ и Д. О. ЛОГОФЕТ

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PREFACE

The last decade has seen a kind of "ecological explosion"—a sharp rise of interest in ecological problems all over the world. And it is not surprising because the notions of "man", "humanity" cannot be separated from the notion of "environment".

Ecology, being a science synthetic in principle (or as it is now said a systems science), uses a wide variety of methods. And it is only natural that one of the most powerful methods of modern natural sciences—the mathematical method—is widely exploited for solving ecological problems. A new science—mathematical ecology—has emerged and rapidly develops.

One of the problems central to ecology in general (and mathematical ecology in particular) is that of ecosystem stability, "steadiness". It is clear that only stable ecosystems may exist for a long time. On the other hand, the limits of stability determine those maximal ecosystem loads, the exceeding of which will lead to an "ecological catastrophe", i.e. the destruction of the ecosystem. The problem of stability always presents itself, when we exploit natural populations and communities, evaluate the environment pollution limits, take into account the implications of certain projects in management of natural resources, or perform appropriate feasibility studies. All these estimates are clear and convincing only if they are quantitative. And that is why we need mathematical models of ecosystems and mathematical methods of their analysis for stability. Here naturally arises the problem of formalization of the term "stability", but this problem is very complicated and far from being accomplished. In general, in mathematical ecology, a science still in its infancy, situations of this kind emerge now and then.

Our book surveys the state-of-the-art in problems of ecosystems stability studied in the framework of their mathematical models. Here we, of course, did not try to cover all the existing approaches and all the variety of models, but took up only the ones that are the most developed and actively discussed in the literature.

A word about the format of the book is in order. Each chapter is opened by an "Ecological Introduction" that briefs the reader on per-

tinent ideas and concepts from ecology tied up with the class of models to be considered. These introductions also outline the possible trends in ecological interpretations of the mathematical results. Not infrequently, these ecological introductions appear necessarily to be ecomathematical ones. Every chapter is concluded by literature references and comments, presented in such a way that the reader could get an idea not only of the origin of the described methods and results, but also of their future development and generalization trends. For confirmation of most of the principles stated in the ecological introduction the reader is referred to the fundamental work by E.P. Odum entitled *Fundamentals of Ecology*, which has been translated into Russian.

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Moscow, 1982

The authors

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INTRODUCTION

It must be intuitively clear that a biogeocenosis, an ecosystem, a biological community, which exists sufficiently long in a more or less invariable state, should possess intrinsic abilities to resist perturbations coming in abundance from the environment (including man). This ability of an ecosystem is usually termed "stability". Though the notion seems obvious, it is quite a problem to provide it with a precise and unambiguous definition. So far, this heavily overworked term found no established ("stable") definition.

Analysing a variety of propositions concerning this problem*, one may class the requirements for different biological systems into some groups—the requirements coming under the head of "stability".

The first is the requirement that a whole geographical region or a landscape be to a certain extent invariable in time. A region may comprise a lot of different biogeocenoses, and the entire regional ecosystem may consist of different, loosely interconnected ecosystems. The main processes that govern regional dynamics are not the population variations in inhabiting species, but rather global biogeochemical cycles.

The second group of requirements concerns preservation of the number of species in a given biological community. A biological community may be thought of as a higher level of living matter organisation, as compared with population, and may be defined as an aggregate of populations making their living on a common territory and showing a certain pattern of food (trophic) interactions and metabolism. The concept of biological community mirrors the fact that populations of living organisms are not randomly distributed throughout the Earth as independent groups but form structured systems. A community is considered to be stable, if the number of member-species remains constant over sufficiently long time intervals. Per-

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* Diversity and stability in ecological systems. In: "Brookhaven Symp. in Biology", No. 22, National Bureau of Standards, US Dept. of Commerce, 1969.
Ecological Stability, Ed. by M. B. Usher, M. Williamson, Chapman and Hall, 1974.

haps, it is this ecological definition that is the closest to various mathematical definitions of stability, and it is precisely for this reason that this book is mainly concerned with stability problems of biological communities.

Finally, the third group of requirements refers rather to individual populations, than to communities. A community is considered to be stable, when numbers of component populations do not undergo sharp fluctuations. This definition is closer to the physical (or rather, thermodynamical) notion of system stability. In thermodynamics a system is believed to be stable, when large fluctuations, which can take the system far from the equilibrium or even destroy it, are unlikely. Evidently, general thermodynamical concepts (for instance, the stability principle associated with the second law of thermodynamics) should be applicable to biological (and, in particular, ecological) systems. By these concepts, any closed system with an energy flow (be it the biosphere, or a small lake) most likely develops towards a stable state, and necessarily feed-back mechanisms set in within the system. When this state is attained, the transfer of energy usually proceeds in one direction and at a constant rate, which corresponds to the thermodynamical stability principle. The predator-prey system is a classic example of such a flow-through system. Unfortunately (and this is true of all overly general concepts), the thermodynamical stability principle gives no effective method to judge about stability of concrete biological communities or ecosystems.

On the other hand, an advanced theory of mathematical stability is available (with a host of applications in science and engineering), in which the definition of stability is absolutely strict. But the point is that this theory deals not with real objects, but with their mathematical models. Therefore, if we have a "good" (from the viewpoint of adequacy and completeness of description) mathematical model of a biological community or an ecosystem (for instance, in terms of differential or difference equations), then the stability of a real community can be deduced from our model by conventional methods of stability theory. However, in mathematical stability theory, too, there exist different definitions for this notion, but this is another question. Stability is generally referred to some solutions of a system of equations, i.e. of a system state, or of its operating regimes. For instance, a community or an ecosystem may be believed to be stable, when its model trajectories in the phase space stay within a given bounded domain for a sufficiently wide scope of perturbations. Such a definition has an intuitive appeal to ecologists who more often than not are happy with it. Granted, here we make a substitution, as we replace the object itself by its mathematical model and for the moment we are not concerned with the question of how adequate is the model to the object modeled. Gnosiologically this approach is justified, since stability analysis of the model enables us to set up

different hypotheses about the laws governing the functioning of the modeled object, whose presence or absence in reality makes it possible to judge among other things about model adequacy.

A principal alternative approach is based on attempts to relate stability of a community to some other characteristic of the community, which can be really (and easily enough) measured. Among ecologists it is taken almost as an axiom, that communities, which are more complex in structure, more rich in comprising species, are necessarily more stable. This seems to be explained in the following way. Different species are differently adapted to variations in environment. Therefore, a variety of species may respond with more success to different environmental variations, than a community of a small number of species, and hence the former will be more stable. Perhaps, this motivates the use of indices of specific diversity (in particular, the information entropy or some of its analogs) as characteristics of community stability. The most popular is the informational *diversity index* (according to Shannon)

$$D = -\sum_{i=1}^{n} p_i \ln p_i, \qquad p_i = \frac{N_i}{N}, \qquad N = \sum_{i=1}^{n} N_i,$$

where n is the number of species in a community, N_i is the population of ith species. Or a somewhat different index:

$$D_1 = 1 - \sum_{i=1}^{n} \frac{N_i(N_i-1)}{N(N-1)}.$$

One may show that D_1 is the probability that two individuals randomly sampled from the collection of N, will not belong to the same species. For big N and fairly uniform distribution in species, $D_1 \approx \approx D$. In fact,

$$D_1 = \frac{N}{N-1}\left(1 - \sum_{i=1}^{n} p_i^2\right) \approx 1 - \sum_{i=1}^{n} p_i^2 = -\sum_{i=1}^{n} p_i(p_i - 1) \approx -\sum_{i=1}^{n} p_i \ln p_i,$$

since $p_i - 1 \approx \ln p_i$. Other definitions of stability measures were suggested (using, for instance, the informational measure proposed by R. Fisher), but all of them, basically, use notions coming from physics or information theory.

It would be logical to suppose that in equilibrium state the community is most stable, and hence should exhibit maximal diversity. But, as it may be readily shown, in this case the community structure is such that specimens of any species occur with the same frequency ($\max\limits_{p_i} D$ is attained at $p_i^* = 1/n$), that is, all species are equally abundant, with no dominating species, and no quantitative

hierarchy in the community. However, observations in real communities (in particular, for most naturally distinguished elementary components of the biosphere—for biogeocenosis) indicate just the opposite: most of the communities that exist long enough (hence stable) involve dominating species, which carry out the major part of work on processing energy and matter in the community, that is, communities have hierarchical structures. This strongly suggests that the diversity as a measure of community stability is not quite justified.

Notice, however, that in numerous laboratory (as well as non-laboratory) communities in the early stages of their evolution towards an equilibrium state, an increase in diversity (i.e. of D) may be observed. Clearly, to a certain extent, this measure still characterizes the community; moreover, this measure in all probability can even characterize its stability, but only in the early stages of evolution.

What is the cause of these paradoxes? Probably, it is the formal application of models from physics and information theory to systems that do not suit them. Both the Boltzmann entropy in statistical physics and the informational entropy in information theory make sense only for ensembles of weakly interacting particles or other objects. The introduction of an entropy measure in such sets is well founded. But as soon as we become concerned with systems of strongly interacting elements, the entropy measure suits no longer. But biological communities, where competitive relations stand out mostly in the vicinity of equilibrium and the whole structure is basically determined by intraspecific interactions and not by intrinsic specific features, represent precisely the systems with strong interactions.

This explains the success in application of entropy measures in early stages of evolution of the communities. The point is that in these stages, which are far from equilibrium, the competition is still weak, its stress is low, and the community may well be regarded as a system with weak interactions.

As seen from the above, there is no explicit answer to the problem of the cause-effect relationship between diversity and stability of a community. Professor E. Odum poses the question on this point: "Is the variety only the spice of life or is it a necessity for the long life of the total ecosystem comprising man and nature?"*

So far we have in no way defined what we mean by community stability, and were satisfied by intuitive insight. But in order to advance further along these lines, we will need to give a formal (yet constructive) definition to this notion.

We shall say that a community is *stable*, if the system of differential (or difference, or differential-difference, etc.) equations, which

* Odum E. *Fundamentals of Ecology*, W. B. Saunders, Philadelphia, p. 256, 1971.

is a model of this community, has a stable non-trivial positive solution. In what follows we shall be mainly concerned with stability of steady-state solutions, such that populations of none of the species neither vanish nor tend to infinity. These solutions will be termed *non-trivial equilibrium* (or often simply *equilibrium*) of the community. Stability of such solutions implies preservation of the number of species in the community (the opposite, generally speaking, is not necessary). Thus, we have formalized one of the ecological definitions of stability.

It is only natural to think that the exclusion of one or several species from the community indicates that the latter is no longer stable. The remaining species can make up a stable community, but then it will be another community.

We have already mentioned that mathematical stability theory has a lot of definitions of stability. One of the basic ones is the stability in Lyapunov's sense. It is this notion that will be most frequently used in this book. Therefore, we assume that our reader is somehow acquainted with the basic ideas and methods of the Lyapunov stability theory.

However, other definitions of stability will be used here, too. For instance, stability is interpreted as boundedness of solutions from below and above (it is often called *stability in Lagrange's sense*). We illustrate this by an example. Let the community be such that the species populations are different from zero and infinity, but there is no stable non-trivial equilibrium. Nevertheless, neither of the species declines to extinction in such a community. This means that model trajectories are bounded from above and below by some positive numbers; however, if stability is considered in Lyapunov's sense, the community is unstable but, on the other hand, it is stable from the viewpoint of preservation of the number of species, i.e. in the sense of the second ecological definition. Therefore in this case we shall speak about *ecological stability* of a community, rather than about its simple stability.

Consider in more detail the requirement of population finiteness. Since unbounded population growth cannot be observed in real communities, such an effect in a model suggests that the model is inadequate (some limiting factors are not included). But adequacy is usually postulated, and though an indefinite population growth of one or several species is by no means equivalent to exclusion of species from the community, this effect, too, may be regarded as a disturbance of stability. This is also confirmed by the following: since the resources coming to an ecosystem are always limited, an indefinite population growth of one of the species would make the resource insufficient for other species, thereby bringing the latter to extinction.

CHAPTER 1

STABILITY OF ISOLATED POPULATION

1.1. Ecological introduction

There is not a single living organism of any species that exists separately from other organisms—all of them form groups which we call *populations*.

Within the populations we find fairly complicated interactions, but in their relations with other populations as well as with the environment they act as some integrated structures. Therefore the lowest level of living matter organisation considered in ecology is the population level.

The basic characteristic of a population is its total *number* or *density* (number of organisms per unit space, occupied by the population). Usually it is expressed in terms of the number of specimens or their *biomass*. The number defines the *size* of the population. It is characteristic that in nature we find specific lower and upper limits to the population sizes. The upper limit is determined by the energy flow in the ecosystem, to which the population belongs; by the trophic level occupied by the population, and by the physiological characteristics of the organisms concerned (the level and rate of metabolism). The lower limit is usually defined only statistically—in the case of too small a population size the probability of fluctuations leading to the complete death of the population increases sharply.

One of the basic ecological principles is the statement that in an unlimited, stationary, favourable environment the population grows exponentially. However, as mentioned above, in nature this is never observed—the population size always has an upper limit. Light, food, space, other organisms, etc., may act as a limiting factor (or limiting factors).

The variation of the total population size is determined by two processes: birth and death. The birth process is characterized by the *birth-rate*—the population's ability to grow in number. The *maximal* (absolute, physiological) *birth-rate* is the maximal possible number of descendants, produced by one specimen in perfect ecological conditions without any limiting factors and only defined by physiological abilities of the organism. *Ecological birth-rate* (or simply *birth-rate*)

is connected with the population growth in really existing environmental conditions. It depends upon the size and composition of the population, as well as upon the physical conditions of the environment.

The process of population decline is characterized by *mortality*. By analogy with birth-rate we distinguish the *minimal* mortality associated with the physiological life period, and the *ecological* mortality describing the probability of a specimen's death in natural conditions. Obviously the ecological mortality by far exceeds the physiological one.

Turning to the dynamics of an isolated population we can assume the birth-rate and mortality indices to be generalized parameters, specifying the interaction of the population and the environment.

1.2. Simplest models of uniform populations. Stability of their steady states

Let us suppose that a population is uniformly distributed in space, all the specimens comprising the population are the same, generations overlap, and the number or density of the population $N(t)$ is a continuous differentiable function. Then the behavior of $N(t)$ can be given by

$$\frac{dN}{dt} = (B - D)\,N, \tag{1.1}$$

where B and D are the birth-rate and mortality, respectively, and in general they may depend on N and t. With $B - D = \varepsilon = \text{const}$ we get the well-known principle of exponential population growth in an unlimited medium (*Malthus principle*). A significant body of experimental evidence suggests, however, that generally populations that are parts of stable ecosystems show a statistically certain negative correlation between ε and N. (It is interesting that the only population, where a positive correlation between these two values has been found, is the human population!) The most simple form for the regression dependence between ε and N is the linear one. Thus we can suppose that $\varepsilon = \alpha - \gamma N$; $\alpha, \gamma > 0$ and the equation for the population dynamics can be written in the form

$$\frac{dN}{dt} = N(\alpha - \gamma N). \tag{1.2}$$

In populations theory this is the well-known *logistic* equation; its solution is

$$N(t) = \frac{\alpha N_0 e^{\alpha t}}{\alpha + \gamma N_0 (e^{\alpha t} - 1)}. \tag{1.3}$$

It is easily seen that $\lim_{t \to \infty} N(t) = \alpha/\gamma$, i.e. the population does not grow infinitely, but is bounded above.

We can separate all the variety of the growth coefficients as functions of the total number into two classes: the first class in which ε decreases steadily with increasing N, and the second class characterized by the disturbances of monotonicity (Fig. 1). The second type

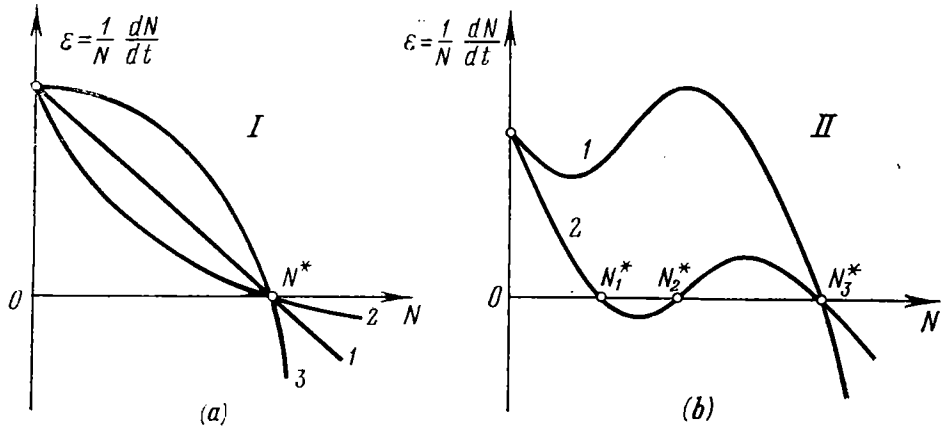

Fig. 1. Two types of relationships between the growth coefficient and population numbers: *I*—monotonic relationship (curve *1* gives the logistic equation); *II*—Alle-type non-monotonic relationship.

of functions is encountered in populations with a clearly expressed team behavior and mutual help, e.g. in populations of colonial birds and animals, which have developed group forms of defence from predator's attacks, common breeding habits and so on. Here when the group effect begins to show up the growth rate starts to increase with N. Then, as the population grows, the general lack of resource begins to tell and the variation of $\varepsilon(N)$ is reversed. This type of behavior is described by the so-called *Alle curve* and results in some new effects, e.g. in the appearance of several stable steady states.

The equilibrium points for the equation

$$\frac{dN}{dt} = \varepsilon(N) \cdot N$$

can be evaluated from the relation $dN/dt = 0$. It is clear that one of these points corresponds to zero population, and the rest are the roots of the equation $\varepsilon(N) = 0$. If the function $\varepsilon(N)$ belongs to the first class, there exists another non-trivial point of equilibrium; in the case of the *Alle*-type function there may exist a number of additional steady states.

For the stability analysis of these states let us use the method of phase diagrams—the graphs of dN/dt as functions of N. The basic as-

sumption here is that the function $\varepsilon(N)$ is single-valued, i.e. each population number corresponds to only one value of ε (the inverse statement might not be true, as for Alle curves, for example). Note, however, that recent data on different reactions of some populations in the growth and degradation phases suggest the possible lack of uniqueness in the $\varepsilon(N)$ relation.

Figure 2 shows the phase diagrams for the functions $\varepsilon(N)$ of the types given on Fig. 1 (*I* and *II*) (curve *2* has several points of equilibrium). From these diagrams we see that in any case the state with

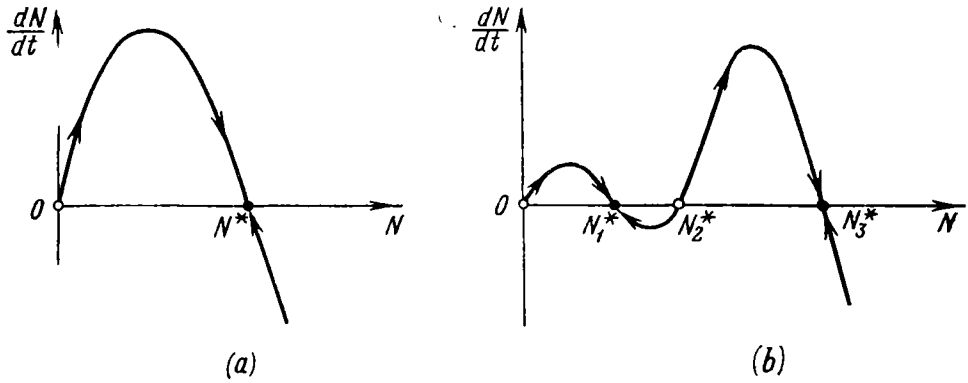

Fig. 2. Phase diagrams for the model $dN/dt = \varepsilon(N)N$ under different forms of $\varepsilon(N)$ behavior (○—unstable point, ●—stable point): (*a*) $\varepsilon(N)$ steadily decreases with N. Whatever the initial non-zero numbers, the population tends to the N^* state; (*b*) $\varepsilon(N)$ is a non-monotone Alle-curve. If $N_0 \in (0, N_2^*)$ the population approaches the N_1^* state; otherwise, when $N_0 \in (N\ , \infty)$ it apdroaches the N_3^* state.

a zero population is unstable. For monotonous functions of the first class the unique non-trivial steady state is stable (in particular, the limiting value for the population $N_\infty = \alpha/\gamma$ in the logistic model is stable). If the $\varepsilon(N)$ relation is represented by an Alle curve, three non-trivial steady states appear, where N_1^* and N_3^* (the smallest and the largest populations) are stable, while N_2^* (the intermediate population) is unstable.

The sufficient conditions for stability and instability are obvious. Indeed, it is seen in Fig. 2, that the stability or instability is related to the sign of the derivative $d[\varepsilon(N)N]/dN$ at the equilibrium point. But

$$\frac{d}{dN}[\varepsilon(N)\cdot N] = \frac{d\varepsilon(N)}{dN}\cdot N + \varepsilon(N) = \frac{d\varepsilon(N)}{dN}\cdot N + \frac{1}{N}\frac{dN}{dt}, \tag{1.4}$$

and as $dN/dt = 0$ at the point $N^* > 0$, the equilibrium point N^* is stable (asymptotically), if $d\varepsilon/dN < 0$ at this point, and unstable if $d\varepsilon/dN > 0$.

The presence of two different stable steady states in populations, characterized by an Alle-type relation, can be interpreted as the appearance of some new form of adaptation to the environment allowing an increase in the population, in other words an extension of the environmental "capacity".

To sum up, let us make clear the following question: is there such a form of the dependence $\varepsilon(N)$, that would provide cyclic population oscillations—a phenomenon often observed in nature? It turns out that there is no such dependence, for otherwise there would be two times t_1 and t_2 with equal N values but different dN/dt, which does not agree with the original model $dN/dt = \varepsilon(N) \cdot N$ and the assumption about the single-valuedness of $\varepsilon(N)$. But if this dependence is not single-valued, relaxation-type oscillations might appear. There may also be other mechanisms responsible for the population oscillations. These will be considered in some detail in later sections.

1.3. Lag-factor and stability of population steady states

Till now we assumed that there was no difference between specimens within the population, and the processes of birth and death took place simultaneously. But in real populations the intensity of these processes is different for different age-groups. For example, in insects the eggs are layed by adults, while the competition is most expressed on the larvae phase. Or to take such processes as the environment intoxication by the metabolism products, cannibalism, etc., which mostly affect the younger age-phases, while their intensity depends on the number of adults, i.e. the coefficient of natural increment is subject to a negative influence by the specimens of the previous generation.

For the logistic population model, accounting for this influence, we can write

$$\frac{dN(t)}{dt} = [\alpha - \gamma N(t-\tau)] \cdot N(t) \tag{1.5}$$

where τ is the average life span for one generation. We still have to set the initial conditions. Let $N(t) = N_0(t)$, $0 \leqslant t \leqslant \tau$, where $N_0(t)$ is a continuous function and $N_0(\tau) > 0$. To a certain extent, this representation can take into account the population age-structure (though in a very rough form).

Just as the logistic equation (1.2), so the equation (1.5) has one non-trivial equilibrium $N^* = \alpha/\gamma$. It would be interesting to know, what are the parameter values required for this equilibrium to be stable (in the model without a time-lag the non-trivial equilibrium is always stable).

The equation (1.5) can be written as

$$\frac{dx(t)}{dt} + \gamma N^* x(t-\tau) = -\gamma x(t)\, x(t-\tau). \tag{1.6}$$

where $x(t) = N(t) - N^*$. Since

$$\frac{|x(t)\cdot x(t-\tau)|}{|x(t)| + |x(t-\tau)|} \to 0$$

as $|x(t)| + |x(t-\tau)| \to 0$, according to the well known theorem about the stability of solutions to the non-linear differential-difference equations (cf. Bellman R., Cooke K. L. *Differential-difference equations*, Academic Press, 1963) the equilibrium N^* will be stable (asymptotically) if the solutions to the linearized equation

$$\frac{dx(t)}{dt} + \gamma N^* x(t-\tau) = 0 \tag{1.7}$$

tend to zero as $t \to \infty$. And for this to be true it is necessary and sufficient for the roots of the characteristic polinomial

$$H(\lambda\tau) = \lambda\tau e^{\lambda\tau} + \gamma N^*\tau = \mu e^{\mu} + \alpha\tau$$

($\lambda\tau = \mu$, $\gamma N^* = \alpha$) to have negative real parts. The transcendental equation $\mu e^{\mu} + \alpha = 0$ has been studied in detail by Wright, who proved that when $0 < \alpha\tau < \pi/2$, $\mathrm{Re}(\mu) = \tau\,\mathrm{Re}(\lambda) < 0$.

It follows that if the condition

$$0 < \alpha < \frac{\pi}{2\tau} \tag{1.8}$$

holds, the non-trivial population equilibrium with a time delay is stable (as well as without time delay). Apparently the inequality (1.8) will always be valid for populations with small natural growth coefficients and short life-cycles.

The asymptotic stability of the equilibrium N^* means that for small enough $q = \max\limits_{0 \leqslant t \leqslant \tau} |N_0(t) - N^*|$, $|N(t) - N^*| \to 0$ as $t \to \infty$, i.e. it is a local property of the solutions to (1.5). Some evidence for global asymptotic characteristics of the solutions of the initial non-linear equation comes from the theorems due to Kakutani and Markus. We will cite them here without proofs (which are very cumbersome) and in somewhat different formulations.

1. If $N_0(t) > 0$, the solutions to (1.5) are bounded from above and below by positive constants at all t values.

2. At big enough t, the curves $N(t)$ and $\dot{N}(t) \equiv dN/dt$ are either monotonic and $N(t) \to N^*$, $\dot{N}(t) \to 0$ or $N(t)$ oscillates about N^*.

3. If $\alpha\tau \leqslant 37/24$, then $N(t) \to N^*$ as $t \to \infty$ (i.e. the equilibrium N^* is asymptotically stable for all initial deviations which leave us on the positive semi-axis).

4. If $\alpha\tau > \pi/2$, the solutions exist which do not tend to N^* as $t \to \infty$.

5. If $\alpha\tau > e^{-1}$, no solution tends monotonically to N^* as $t \to \infty$.

6. If $\alpha\tau \leqslant e^{-1}$, there are no such oscillating solutions, for which the intervals between zeros of the function $N(t) - N^*$ would be greater or equal to the time delay τ for big enough t.

7. For all $\alpha\tau > \pi/2$ there are non-constant periodic solutions.

These theorems determine the qualitative behavior of the solutions (1.5) at large t for all the values of the natural growth coefficient and the generation duration, related by one parameter $\alpha\tau$. The value of $\alpha\tau$ increases with increasing fertility and length of life. With $\alpha\tau \leqslant 1/e$ the lag-system behavior differs but little from the dynamics of a system without time delay: though in this case population oscillations might occur, their period does not exceed the duration of two generations. When $1/e \leqslant \alpha\tau \leqslant 37/24$ there are always population oscillations, but without perturbations these oscillations decay whatever the initial perturbations might be (naturally if they do not bring the whole population to destruction). If $37/24 < \alpha\tau < \pi/2$ the population exhibits a peculiar transient state, in which for sufficiently small deviations from the equilibrium, $N(t) \to N^*$ as $t \to \infty$, but there may be such deviations, after which the population never returns to the state of equilibrium. Finally, when $\alpha\tau > \pi/2$ there is not a single stable equilibrium in the population, the population may vary in the most irregular way, remaining, however, bounded and oscillating about the N^* value. Such a behavior of $N(t)$ resembles the picture of the "random" population fluctuations, observed in many real populations of high-fertility organisms (e.g. in some insect populations).

Since in this last case, in spite of the absence of a stable equilibrium, $N(t)$ does not become zero at any t values, we can speak here about the *ecological stability*, as the population may exist indefinitely without extinction. However, the factors responsible for a lag in the system diminish the "stability reserve" of the non-trivial equilibrium, restricting the stability domain in the parameter space.

1.4. Influence of random perturbations on population stability

If the population evolution could be precisely described by the above equations, then under definite conditions the population with time would come to the neighbourhood of one of the stable states and would stay there indefinitely. However, there always exist random perturbations of non-regular nature which can force the population to leave the neighbourhood of the stable equilibrium, for instance, to switch from a non-trivial equilibrium to a trivial one, the latter corresponding to the extinction of the population.

In what sense can we speak here about population stability? Different definitions are possible. For example, we can speak about the average residence time of the population in some neighbourhood of the non-trivial equilibrium or about the degeneration probability for a population. The greater the time or the less the probability, the more stable is the population.

Note that if earlier we were speaking about the stability of some equilibrium, now we are dealing with the stability of the population and the measure of this property. Naturally this measure itself will depend on the initial or present population state. Unfortunately the term stability is so much overworked, that often it is even hard to understand what is meant by stability. Further on wherever possible we will try to avoid ambiguity, providing the term "stability" with some additional definition.

The most dangerous from the point of view of population's degeneration is the period of logarithmic growth, when the number of specimens in the population is very small. The deterministic equation describing this phase is the Malthus equation

$$\frac{dN}{dt} = \varepsilon(t) N. \tag{1.9}$$

We can distinguish two factors affecting the population growth. The first one is the random fluctuations of the natural growth coefficient, and the second is the random fluctuations of the population itself. Both may be caused by the environment random variations.

In what way do the random fluctuations of ε influence the population dynamics? Suppose the ε values at different times are mutually independent. Then if $\varepsilon(t)$ at each instant t are normally distributed with the mean $\bar{\varepsilon}$ and variance σ^2 that are independent of time, then according to the Central Limit Theorem $\int_0^t \varepsilon(\tau)\, d\tau$ is also normally distributed with the mean $\bar{\varepsilon} t$ and variance $\sigma^2 t$. And since

$$\frac{N(t)}{N_0} = \exp\left\{\int_0^t \varepsilon(\tau)\, d\tau\right\},$$

the quantity N/N_0 must have a logarithmically normal distribution with the same mean and variance, i.e. with the distribution density

$$f\left(\frac{N}{N_0}\right) = \frac{N_0}{\sigma N \sqrt{2\pi t}} \exp\left\{-\frac{\left(\ln\frac{N}{N_0} - \bar{\varepsilon} t\right)^2}{2\sigma^2 t}\right\}. \tag{1.10}$$

This distribution has one maximum at $N_{max} = N_0 \exp\{(\bar{\varepsilon} - \sigma^2)\, t\}$. It follows at once that if $\bar{\varepsilon} < \sigma^2$ then $N_{max} \to 0$ as $t \to \infty$ and the

distribution mode shifts to the left, while for $\bar{\varepsilon} > \sigma^2$ it shifts to the right. Such a distribution behavior indicates that for $\bar{\varepsilon} < \sigma^2$ the degeneration probability increases with time, approaching unity in the limit—the population is stochastically unstable. It means that being subject to such perturbations long enough the population most probably will decline to extinction. When $\bar{\varepsilon} > \sigma^2$ the degradation probability decreases and as $t \to \infty$ tends to zero—the population is stable in this sense.

Biologically, the result obtained is quite obvious, but it is interesting that it imposes even more strict constraints on the natural growth coefficient than the deterministic model. Indeed, in the latter for the population not to degenerate it is sufficient for the mean value $\bar{\varepsilon} = \frac{1}{t}\int_0^t \varepsilon(\tau)\,d\tau$ to be positive, while in the stochastic model it is not so—it is required that $\bar{\varepsilon} > \sigma^2 > 0$.

How do random fluctuations of the population number influence the growth? We will start off with a well-known physical model. The fluctuation mean amplitude is generally taken to be proportional to $\sqrt{N}$, and the fluctuations themselves at each instant of time are described by the distribution $\varphi(t)$ with a zero mean and variance σ_φ^2. Moreover, we assume the values of $\varphi(t)$ at different times to be mutually independent. Then instead of (1.9) we get

$$\frac{dN}{dt} = \varepsilon N + \varphi(t)\sqrt{N}. \tag{1.11}$$

Introducing a new variable $\eta = 2\sqrt{N}$ we can rewrite (1.11) in a linear non-uniform form

$$\frac{d\eta}{dt} = \frac{1}{2}\varepsilon\eta + \varphi(t) \tag{1.12}$$

with the solution

$$\eta(t) = \eta_0 e^{\varepsilon t/2} + \int_0^t \varphi(\tau) e^{\varepsilon(t-\tau)/2}\,dt \tag{1.13}$$

(assuming $\varepsilon = \text{const}$). The mean of η is

$$\bar{\eta} = \bar{\eta}_0 e^{\varepsilon t/2}, \tag{1.14}$$

since $\bar{\varphi}(t) \equiv 0$, and $\bar{\eta}_0$ is the mean value of the initial conditions $\eta_0 = 2\sqrt{N_0}$ which are also defined by a distribution. However we will take the variance η_0 to be zero. Then the variance of $\eta(t)$ will be

$$\sigma^2[\eta(t)] = \sigma_\varphi^2(e^{\varepsilon t} - 1). \tag{1.15}$$

We used the Central Limit Theorem to derive expressions for the mean and variance, considering that $\varphi(t)$ values are mutually independent.

If $\varphi(t)$ is normally distributed, η also has a normal distribution with the mean given by (1.14) and variance by (1.15). And since

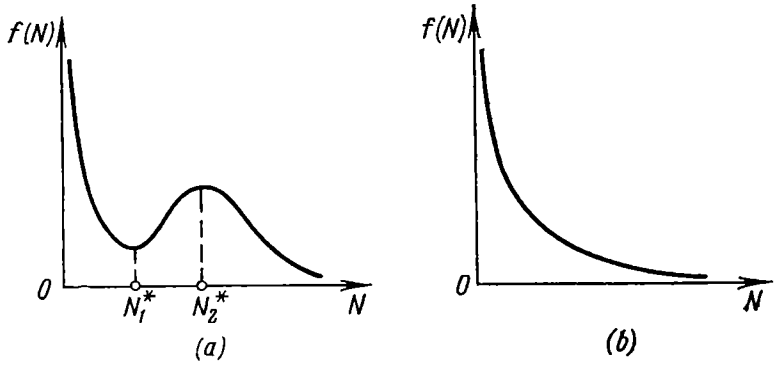

Fig. 3. The population density distribution in the model of exponential growth.

$N = 1/4\eta^2$ the population should have a non-central χ^2 distribution with the non-centrality parameter $\bar{\eta}(t)$. The density of this distribution is

$$f(N) = \frac{Ce^{-\alpha N}}{\sqrt{N}} \{e^{ab\sqrt{N}} + e^{-ab\sqrt{N}}\}, \tag{1.16}$$

where

$$C = \frac{\exp\left\{-\frac{\bar{\eta}^2}{2\sigma^2(\eta)}\right\}}{\sigma(\eta)\sqrt{2\pi}}, \qquad a = \frac{2}{\sigma^2(\eta)}, \qquad b = \bar{\eta}. \tag{1.17}$$

The density $f(N) \to \infty$ as $N \to 0$, but $f(N) \to 0$ as $N \to \infty$. This distribution can either have two extrema (Fig. 3*a*), or steadily decrease to zero with increasing N (Fig. 3*b*). The extrema are found from

$$(ab\sqrt{N} - 2a\sqrt{N} - 1)\, e^{ab\sqrt{N}} = (ab\sqrt{N} + 2aN + 1)\, e^{-ab\sqrt{N}}. \tag{1.18}$$

Since we cannot obtain the exact solutions for (1.18), let us simplify the problem by assuming that $\exp\{-ab\sqrt{N}\} \ll 1$. Then

$$N^*_{1,2} = \frac{1}{16}\left(b \pm \sqrt{b^2 - \frac{8}{a}}\right)^2, \qquad N^*_1 < N^*_2. \tag{1.19}$$

There is a minimum of the distribution at N^*_1, and a maximum at N^*_2. The mean value of N is

$$\bar{N} = \frac{1}{4}[\eta^{-2} + \sigma^2(\eta)] = N_0 e^{\varepsilon t} + \frac{\sigma^2_\varphi}{4\varepsilon}(e^{\varepsilon t} - 1), \tag{1.20}$$

whence, by (1.17) is follows that $N_2^* < \bar{N}$, i.e. the most probable population size is always below its mean size. The ultimate population N_1^* is the least probable. It appears as a kind of threshold, so that if the population declines below $N_1^* = N_{cr}$, the extinction probability increases sharply. Note that N_1^* and N_2^* also increase with t.

It is seen from (1.19) that the distribution $f(N)$ has extrema only if $ab^2 > 8$ or $\sigma^2(\eta) < \bar{\eta}^2/4$. As $\sigma^2(\eta)$ increases the difference between extrema decreases, and they disappear when $\sigma^2(\eta) > \bar{\eta}^2/4$ and $f(N)$ becomes a steadily declining function. The extinction will be the most probable population state, thus suggesting that the population is unstable with respect to random fluctuations of its number. How can it occur? From $\sigma^2(\eta) > \bar{\eta}^2/4$ for sufficiently big t or ε ($e^{\varepsilon t} \gg 1$) we have

$$\sigma^2(\eta) = \frac{\sigma_\varphi^2}{\varepsilon}(e^{\varepsilon t} - 1) \simeq \frac{\sigma_\varphi^2}{\varepsilon} e^{\varepsilon t} > N_0 e^{\varepsilon t}$$

or

$$\sigma_\varphi^2 > \varepsilon N_0. \tag{1.21}$$

In other words, if the fluctuation amplitude is big enough, while the natural growth coefficient and the initial number are small, the population will decline to extinction almost for sure.

Notice that [as follows from (1.20)] on the average fluctuations augment the population growth.

1.5. Random perturbations and logistic growth

Consider a population whose deterministic dynamics is described by a logistic equation. To analyse the action of different perturbations, we will turn to the diffusion approximation of the stochastic Markov process. Omitting the details of the model's deduction, we can say that the probability density $\varphi(N, t)$, where $\varphi(N, t)\,\Delta N$ is the probability that at time t the population number falls into the interval between N and $N + \Delta N$, obeys the Fokker-Planck equation

$$\frac{\partial \varphi}{\partial t} = \frac{1}{2}\frac{\partial^2}{\partial N^2}\{D(N)\varphi\} - \frac{\partial}{\partial N}\{M(N)\varphi\} \tag{1.22}$$

where $M(N)$ characterizes the average evolution trend for the stochastic process $N(t)$, i.e. the population variations, during small time intervals. For $M(N)$ we can take the right-hand side of the deterministic logistic equation, so that

$$M(N) = \alpha N - \gamma N^2,$$

or in a slightly different form ($\alpha/\gamma = K$),

$$M(N) = \alpha N\left(1 - \frac{N}{K}\right). \tag{1.23}$$

Since in the deterministic model $N(t) \to \alpha/\gamma = K$, as $t \to \infty$ K is often referred to as the *carrying capacity of the environment* for a given population. The quantity $D(N)$ characterizes the root mean-square deviation of the process from its mean and is specified in a variety of ways according to the different chosen "models" of randomness.

The limit distribution $\Phi(N)$ should be independent of t, and therefore from (1.22) at $d\varphi/dt \equiv 0$ we get

$$\frac{1}{2}\frac{d^2}{dN^2}\{D\Phi\} = \frac{d}{dN}(M\Phi). \tag{1.24}$$

The solution to this equation should be the probability density, that is

$$\int_0^\infty \Phi(N)\,dN = 1, \qquad \Phi(N) \geqslant 0. \tag{1.25}$$

Besides, if $D(N) = 0$ for some $0 \leqslant N \leqslant \infty$ [in this case a singularity appears: the diffusion term in (1.22) becomes zero], a part of the limit probability may be concentrated in these singular points, and then

$$\lim_{t\to\infty} \varphi(N, t) = \mu\Phi(N), \tag{1.26}$$

where $0 \leqslant \mu < 1$, and $\Phi(N)$ is completely defined on the axis $[0, \infty)$, except for the singular points.

The solution to (1.24) is

$$\Phi(N) = \frac{C}{D(N)} \exp\left\{2\int \frac{M(N)}{D(N)}\,dN\right\}, \tag{1.27}$$

where the constant C is determined from the normalization condition (1.25)

$$C = \left[\int_0^\infty \left(\frac{1}{D(N)} \exp\left\{2\int \frac{M(N)}{D(N)}\,dN\right\}\right) dN\right]^{-1}. \tag{1.28}$$

Since only the qualitative behaviour of the distribtion is of interest, in what follows we will not bother with the calculation of particular values for the normalization constant.

Consider a situation where a logistic population has a natural growth coefficient α that is a random variable with the mean $\bar{\alpha}$ and constant variance σ_α^2. Then

$$M(N) = \bar{\alpha}N\left(1 - \frac{N}{K}\right), \qquad D(N) = \sigma_\alpha^2 N^2\left(1 - \frac{N}{K}\right)^2. \tag{1.29}$$

Inserting (1.29) into (1.27) and integrating we get the limit distribution

$$\Phi(N)=\frac{CN^{2(v-1)}}{\sigma_\alpha^2\left(1-\frac{N}{K}\right)^{2(v+1)}}, \qquad v=\frac{\bar{\alpha}}{\sigma_\alpha^2}. \tag{1.30}$$

Since $D(N^*_{1,2})=0$ at points $N_1^*=0$ and $N_2^*=K$, a part of the limit probability might be concentrated at them. The distribution $\Phi(N)$ itself tends to infinity as $N\to K$ and, if $v<1$, as $N\to 0$ too.

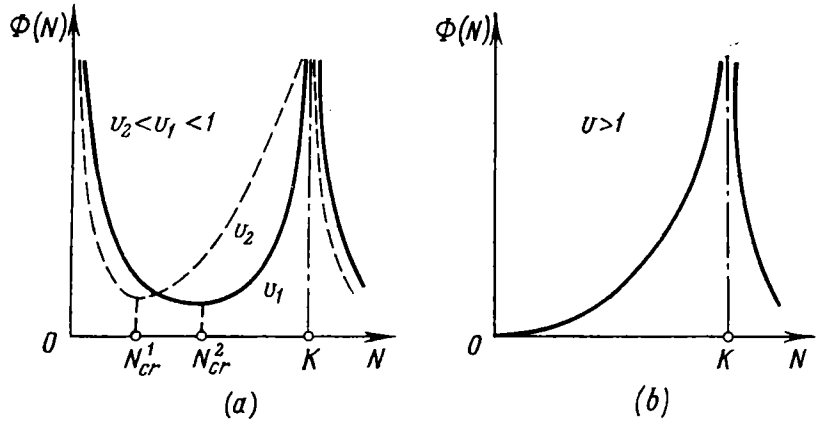

Fig. 4. Density of stationary distributions in the logistic model

When $v<1$ the distribution has a U-shape form (Fig. 4*a*), tending to 0 and K. It follows that the most probable population numbers are either close to zero and the population is likely to decline to extinction, or close to the non-trivial stable equilibrium and the population maintains itself. We can take the least probable population number to be the value $N_{\rm cr}$, which in a sense separates the two limit states of the population, that is

$$\Phi(N_{\rm cr})=\min_{N\in[0,K]}\Phi(N)$$

hence

$$N_{\rm cr}=N_{\rm min}=\frac{K(1-v)}{2}.$$

It is easy to see that when $v\to 0$ (i.e. if $\bar{\alpha}\to 0$ or $\sigma_\alpha^2\to\infty$) $N_{\rm cr}\to K/2$ and the population which passes this border has a lot of chances to avoid extinction. As the mean coefficient of natural growth increases or its variability decreases this barrier is lowered. Finally, if $v\geqslant 1$ it disappears. It can be seen from the $\Phi(N)$ behaviour, which loses its U-shape when $v\geqslant 1$ and concentrates near K (see Fig. 4*b*), and when $v>1$ $\Phi(0)=0$, this making extinction impossible.

Quite a natural result, since when σ_α^2 decreases (and respectively v grows) random α oscillations gradually lessen their influence on the system dynamics, while $N^* = K$ is the system's stable equilibrium. Consequently, when $\bar{\alpha} > \sigma_\alpha^2$ $(v > 1)$ there is no extinction in the population. Notice that this result is similar to the one obtained in the previous section for an unlimited population.

Consider now the influence of random population fluctuations on either of its limit states. The function $M(N)$ remains the same, but to define $D(N)$ we will again use the physical model with the fluctuation amplitude proportional to $\sqrt{N}$. Then for the mean-square deviation $D(N)$ we have

$$D(N) = \sigma_\varphi^2 N, \tag{1.31}$$

where σ_φ^2 is the variance of a given random variable with a zero mean. Substituting $M(N)$ and $D(N)$ into (1.27) we get

$$\Phi(N) = \frac{C}{\sigma_\varphi^2 N} \exp\left\{\frac{2\alpha N}{\sigma_\varphi^2}\left(1 - \frac{N}{2K}\right)\right\}. \tag{(1.32)}$$

$\Phi(N) \to \infty$ as $N \to 0$ and a part of the limit probability might be concentrated at the zero point. The distribution itself resembles a lot the one obtained in the similar case for the non-limited population (cf. Fig. 3). (Note that the following deductions will also be similar.)

For $\sigma_\varphi^2 < \alpha K$ the distribution has the form as shown in Fig. 3*a*. The maximum of $\Phi(N)$ is attained at the point

$$N_2^* = \frac{K}{2} + \sqrt{\left(\frac{K}{2}\right)^2 - \frac{\sigma_\varphi^2 K}{2\alpha}}, \qquad N_2^* < K,$$

whence it follows that the most probable population numbers (when there is no extinction) will always be below the non-trivial equilibrium maintained when there are no random fluctuations. The minimum $\Phi(N)$ is attained at the point

$$N_1^* = N_{cr} = \frac{K}{2} - \sqrt{\left(\frac{K}{2}\right)^2 - \frac{\sigma_\varphi^2 K}{2\alpha}}.$$

If the population declines below N_{cr}, the probability of population extinction rises sharply. It is easily seen that this threshold lowers with increasing natural fertility and decreasing fluctuations amplitude.

When $\sigma_\varphi^2 > \alpha K$, i.e. when the fluctuation amplitude is high, but the natural growth coefficient and the carrying capacity are low $\Phi(N)$ has the form shown in Fig. 3*b*. Degeneration will be the most probable population state and sooner or later the population will decline to extinction.

And finally, let us look at the case where random perturbations change the carrying capacity K of the environment, so that K is equal to some random variable $K(t)$ with the mean $\bar{K}$ and constant variance σ_K^2. The values of $K(t)$ at different times are mutually independent. However, it would better suit our purpose to consider instead of $K(t)$ the variable $\varkappa(t) = 1/K(t)$ with the mean $\bar{\varkappa}$ and variance $\sigma_\varkappa^2$, and instead of the random population $N(t)$ the variable $\xi(t) = 1/N(t)$. For these variables the logistic equation can be represented as a linear non-uniform equation

$$\frac{d\xi}{dt} = \alpha[\varkappa(t) - \xi]. \tag{1.33}$$

The solution to this equation in terms of the original variables is

$$N(t) = \frac{N_0 e^{\alpha t}}{1 + \alpha N_0 \int\limits_0^t \frac{d\tau}{K(\tau)\, e^{-\alpha\tau}}} \tag{1.34}$$

This expression shows that the population numbers depend upon the weighted harmonic mean of the random carrying capacity. Since $M(\xi) = -\alpha\xi + \alpha\bar{\varkappa}$, $D(\xi) = \alpha^2\sigma_\varkappa^2$ the limit distribution is

$$\Phi(\xi) = C \exp\left\{-\frac{\xi^2 - 2\bar{\varkappa}\xi}{\alpha\sigma_\varkappa^2}\right\}$$

or

$$\Phi(\xi) = C_1 \exp\left\{-\frac{(\xi - \bar{\varkappa})^2}{\alpha\sigma_\varkappa^2}\right\}, \tag{1.35}$$

that is, the variable $\xi = 1/N$ is normally distributed with the mean $\bar{\xi} = \bar{\varkappa}$ and variance $\alpha\sigma_\varkappa^2/2$. Since $1/\bar{\varkappa}$ is the harmonic mean H_K for the carrying capacities

$$\frac{1}{\bar{\varkappa}} = H_K = t \Big/ \int\limits_0^t \frac{d\tau}{K(\tau)},$$

and since $H_K < K$ (at $\sigma_K^2 > 0$), the population distribution median, which is equal to H_K, will be always below the mean values of the carrying capacity. In other words, with randomly fluctuating environment its effective carrying capacity (i.e. the most probable steady state population) will always be less than its mean carrying capacity, with their difference increasing with α. This statement follows from the equation well-known in statistics relating the harmonic (H) and arithmetic (M) means of a given random variable:

$$H = M\left(1 - \frac{\sigma^2}{M^2}\right). \tag{1.36}$$

1.6. Average life time of a population

Consider a situation where a population is affected by perturbations of low intensity as compared with dynamic factors influencing its evolution. Let this evolution be described by the deterministic equation

$$\frac{dN}{dt} = f(N), \tag{1.37}$$

or, to be more specific, the logistic equation

$$f(N) = \alpha N\left(1 - \frac{N}{K}\right).$$

Let the random perturbations at different times be independent and uniform in time, i.e. they can be described by a "white noise"-type process ζ_t. Then

$$\frac{dN}{dt} = f(N) + \varepsilon\zeta_t, \tag{1.38}$$

where $\varepsilon > 0$ is a small parameter characterizing the smallness of random perturbations. Let a system be near a stable equilibrium N_1^* and Ω_1 is the attraction domain of this point. Then, as a measure of stability of this equilibrium against random perturbations we can take the mean time τ_1 needed for the trajectory initiated in Ω_1 to leave Ω_1. Since τ_1 is a random variable, it would be natural to consider the mathematical expectation $\bar{\tau}_1$ of this variable. To obtain $u(N) = \bar{\tau}_1$ we can formulate a boundary-value problem, however this problem proves to be fairly complicated and the measure obtained is too cumbersome. Therefore for small ε it would be natural to use the principal term $\bar{\tau}_1$, as $\varepsilon \to 0$ as the measure of stability. It turns out that

$$\bar{\tau}_1 \simeq \exp\left\{\frac{c_1}{2\varepsilon_2}\right\}, \tag{1.39}$$

where c_1 is a constant, which defines the measure of stability for random fluctuations $\varepsilon\zeta_t$. Let us describe the calculation method for this constant. It appears that if we write $f(N)$ as

$$f(N) = -\frac{d}{dN}V(N), \tag{1.40}$$

that is we introduce a quasi-potential V, then

$$c_1 = \min_{N \in \partial\Omega_1} 4V(N), \tag{1.41}$$

where $\partial\Omega_1$ is the boundary of Ω_1.

If $f(N)$ has a logistic form, then

$$V(N) = -\frac{\alpha N^2}{2} + \frac{\alpha N^3}{3K} + A, \quad \text{where } A = \text{const}. \tag{1.42}$$

The population has a stable equilibrium $N_1^* = K$ with the domain $\Omega_1 = (0, \infty)$ and an unstable one $N_2^* = 0$. Obviously, (1.41) attains the minimum at the point $N = 0$ and $c_1 = 4A$. The equality $V(N_1^*) = 0$ gives the integration constant A. From (1.42) at $N = N_1^* = K$ we find that $A = \alpha K^2/6$. Then

$$\bar{\tau}_1 \simeq \exp\left\{\frac{\alpha K^2}{3\varepsilon^2}\right\}. \tag{1.43}$$

This expression shows that as the natural growth coefficient α and the carrying capacity K increase, the mean life time of the population grows, with the carrying capacity being more important for the survival. If we rewrite the logistic equation in another form, i.e. in terms of the coefficient of interspecific competition ($f = \alpha N - \gamma N^2$), then

$$\tau_1 \simeq \exp\left\{\frac{\alpha^3}{3\gamma^2\varepsilon^2}\right\}. \tag{1.44}$$

The interpretation of this relation is also quite obvious: intensification of interspecific competition reduces the mean life time, however this effect is not so clearly pronounced as the natural growth decline having the same implications.

The example considered shows that even small, but constant, perturbations can "shatter" and destroy the population, while without perturbation it could exist indefinitely.

1.7. Deterministic and stochastic models

The results of the three previous sections indicate that the general implications of the consideration of random factors in the mathematical models in population theory (and apparently also in the theory of biological communities) are more rigid requirements imposed on the system parameters responsible for system stability (in some sense or other). Naturally, the stability domain determined by some criterion based on a stochastic model, will be smaller than its counterpart for a deterministic model.

Questions arise, "Under what conditions do the deterministic models describe the real-life situations more or less adequately and when can the stochastic effects be neglected?"

We usually suppose that the community at hand consists of n groups (populations) with numbers $N_1, N_2, \ldots, N_n$. If we know

these numbers at time of interest, then we think that thereby we completely define the community dynamics. Generally speaking, we can treat $N_1, N_2, \ldots, N_n$ as random variables and describe their time variations as a stochastic process, with $P(t; N_1 \leqslant \bar{N}_1, \ldots, N_n \leqslant \bar{N}_n)$ being the probability that the community numbers no more than $\bar{N}_1, \ldots, \bar{N}_n$ specimens from the appropriate groups at a given time instant. Since as the population grows the random variables $N_1, \ldots, N_n$ converge in probability to their mean values, the behavior of the sufficiently large community is adequately described by the dynamics of means. Therefore this book, dealing with one aspect of the communities dynamic behavior—the stability, concentrates on fairly large communities, which we describe by mathematical expectations (means) of the group number.

There may be a more "physical" approach to this problem, which has almost nothing to do with the stochastic concepts. Let $\{N_1, \ldots, N_n\}$ be an n-dimensional phase space, and in this space we are examining the curves which are the trajectories of our model system. The real system behaviour can be presented as a movement along some perfect averaged trajectory with different superimposed fluctuations. But the residence time for states differing from the mean is proportional to $1/\sqrt{\sum_{i=1}^{n} N_i}$. Accordingly, we can assume that at sufficiently big total numbers the community almost always (but maybe for some isolated instants of time) moves along the perfect trajectory. Therefore for large communities the dynamic description is suitable.

Certainly these speculations cannot claim to be rigorous. But they are plausible enough and they seemingly provide the clues as to the choice of formalization for the object being modeled.

1.8. Notes and bibliography

To 1.2. A lot of models of dynamics of an isolated population have been created. In the book:

Watt K. E., *Ecology and Resource Management. A Quantitative Approach*, McGraw-Hill, New York, 1968

about thirty different population models are selected and even a dichotomous classification tree is built. We have confined ourselves to a more or less detailed investigation of only one, perhaps the most simple, model—the *logistic* one, though we know of W. Feller's unfavourable opinion of this model (see

Feller W., *An Introduction to Probability Theory and its Applications*, Wiley, New York).

In essence, this characteristic is aimed against an absolutization of the logistic equation, the declaration of the logistic growth as some general biological principle. As for us, we consider the logistic model just as a convenient and simple phenomenological description of really observed effects in growing populations.

Tanner J. T., "Effects of population density on growth rates of animal populations," *Ecology*, 47, 5, p. 733-745, 1966

discovered a statistically certain negative correlation between the relative growth rate and density in 45 of 63 analyzed populations of insects and vertebrates (according to data from the literature). Interestingly, the only population that always demonstrates a positive correlation is the human one. True, populations are known that exhibit positive correlation for some densities, but it again becomes negative when the population density rises further. This so called "Alle principle", postulating a non-monotone relationship between the relative growth rate and population density for populations of some species with a clearly expressed group behaviour, was first formulated in the book.

Alle W. C., *Animal aggregations: a study in general sociology*, Chicago Univ. Press, Chicago, 1931.

A detailed treatment (from the ecological viewpoint) of different types of these relationships is given in:

Alle W. C., Emerson A. E., et al., *Principles of Animal Ecology*, Saunders, Philadelphia, 1949.

To 1.3. V. A. Kostitzin was the first to highlight the role of time delays in population models and new dynamic effects in them:

Kostitzin V. A., *Symbiose, parasitisme et evolution*, Herman, P., 1934.

The equation $\mu e^{\mu} + \alpha = 0$ is analysed in the paper:

Wright E. M., "Stability criteria and real roots of a transcendental equation," *SIAM J.*, 9, 2, pp. 136-148, 1961.

A more detailed treatment of the results presented in this section can be found in:

Kakutani S., Markus L., *On the Nonlinear Difference-Differential Equation* $y'(t) = [A - By(t - \tau)]\, y(t)$, Princeton Univ. Press, Princeton, pp. 1-18, 1958—(Contributions to the theory of nonlinear oscillations, V. 4); Jones G. S., "Asymptotic behavior and periodic solutions of a nonlinear differential-difference equation," *Proc. Nat. Acad. Sci. USA*, 47, 6, pp. 879-882, 1961.

To 1.4-1.5. Here we have described the results obtained in the paper:

Levins R., "The effect of random variation of different types on population growth," *Proc. Nat. Acad. Sci. USA*, 62, 4, pp. 1061-1065, 1969,

and in the book:

Svirezhev Yu. M., Yelizarov, E. Ya., *Mathematical Modelling of Biological Systems*, Nauka, Moscow, 1972, pp. 135-138. (*Problems of space biology*, Vol. XX) (in Russian).

To 1.6. The analytical methods for fairly large dynamic systems under small random perturbations are presented in:

Ventzel A. D., Freidlin M. I., "On small random perturbations of dynamical systems," *Uspekhi Mat. Nauk* 25, 1, pp. 3-55, 1970 (in Russian),

and the applications of this method to two types of population models are discussed in:

Freidlin M. I., Svetlosanov V. A., "On the effect of small random perturbations on the ecological systems state stability," *Journal of General Biology*, 37, 5, pp. 715-721, 1976 (in Russian).

To 1.7. When can we use deterministic, and when stochastic, models?—this is one of the key questions not only in ecology or population genetics, but for instance in physics as well. And this problem is far from its solution. While in physics the situation is better suited to a stochastical approach, since we deal with quantities of the orders of magnitude of 10^6-10^{12}; in ecology and in genetics we encounter orders of magnitude of 10^2-10^3. It is too much for an individual description, but it is still not enough for the statistical properties to show up clearly. Nevertheless, because there is no adequate mathematical tool, models

originating from statistical physics are widely used in mathematical ecology. Numerous models of this kind are summarized in a review article:

Goel N. S., Maitra S. C., Montroll E. W., "On the Volterra and other nonlinear models of interacting populations," *Rev. Mod. Phys.*, **43**, **1**, pp. 231-276, 1971.

The problem of ecosystem stability for random porturbations is discussed in:

Verigo V. V., Svirezhev Yu. M., *Some problems of biosystem construction*, In: "Proceedings of IV Readings in Memory of K. E. Tsialkovsky", Moscow, State Cosmonautics Museum, pp. 7-12, 1972 (in Russian).

There you can also find a formulation of a peculiar analog of the complementation principle for the procedure of the ecosystem trajectory evaluation.

CHAPTER 2

DISCRETE POPULATION MODELS

2.1. Ecological introduction

In the models of the previous chapter we have looked at the population development in continuous time and, what is more, the population numbers have been presented as solutions to differential equation, i.e. as continuous functions. Such a scheme calls for some assumptions about the population itself, in particular, it should be numerous enough to allow a continuous approximation. Moreover, the form of ordinary differential equations presupposes that the number variations at every time t only depend upon their instantaneous values at that same time. We can get along with such an assumption only in a small number of special cases, while in most natural populations the delayed effects of the number regulating factors prove to be fairly important. When the population is simulated by a continuous function $N(t)$, these effects are included in the differential equations with lagging arguments—they were touched upon in Section 1.3.

It is clear, however, that a presentation of a population in the form of a discrete variable N_t, taking on different values at fixed times, is more realistic. This scheme exactly reflects the census-taking process for natural populations (in laboratory or field studies), which is usually realized at discrete points in time. The natural assumption about the population N_t being dependent upon its numbers at some preceeding times—one of the forms of accounting for time-lags—leads to the use of the mathematical tool of difference equations. A difference equation of order k has the form

$$N_t = F(N_{t-1}, N_{t-2}, \ldots, N_{t-k}; t), \tag{2.1}$$

where the parameters of the function F in the general case depend upon the time step t. For a population this might denote a variation in time of external and internal factors determining its development. But if we can assume that these factors remain constant over a given time period, we get the equation with the right hand side constant in time

$$N_t = F(N_{t-1}, N_{t-2}, \ldots, N_{t-k}), \tag{2.2}$$

that is the population at time t depends in some definite (fixed) way only upon its number at k preceeding times.

The idea to use difference equations is most tempting when the number of every successive generation N_{t+1} depends only on the number of the previous generation N_t. Such a situation occurs, for instance, in populations with no overlapping generations and no long diapauses in the life-cycle. In particular, a lot of insect species fall into this category. Adults in their populations live for a short time, which is enough for them to lay eggs, and when the new generation reaches the grown-up stage, the previous one already declines to extinction. For such populations the postulate of non-overlapping of generations is accepted without any doubt; for other populations it can be accepted as an approximation.

If generations overlap significantly or at some stage a significant part of the population is layed aside in diapause for a length of time that exceeds the life-span of one generation, the assumption of N_{t+1} being a function of N_t alone is no more valid.

It is already clear from these remarks that when dealing with a lot of populations, we should bear in mind that populations naturally split into discrete age-classes (or development phases) whose numbers depend on the numbers of the preceding, and sometimes of all the other, age-classes. And the problem of the evaluation of age-structure dynamics is reduced to the analysis of another discrete system—this time a matrix one.

What is behavior of discrete models (difference equations and matrix systems) that corresponds to population stability and what are the analytical methods and conditions of this stability? These are the questions we will try to answer in this chapter.

2.2. Population models with non-overlapping generations

For populations with generations that may be considered non-overlapping (if the main environmental properties are unchanging), equation (2.2) transforms into the first order equation

$$N_{t+1} = F(N_t) \tag{2.3}$$

or in a more familiar form

$$N_{t+1} = N_t \cdot f(N_t). \tag{2.4}$$

Some restrictions on F immediately follow from obvious considerations. Since for biological reasons $N_t \geqslant 0$, clearly $F(N) \geqslant 0$ for all possible $N > 0$ and F gives a one-to-one self-mapping of the semi-axis $[0, \infty)$. Naturally $F(0) = 0$, and at small N the population increases, that is in some neighborhood of zero $F(N)$ is an increasing function. On the other hand, resource limitations require that

$F(N) \to 0$, as $N \to \infty$. A typical form of $F(N)$ behavior is shown in Fig. 5*a*.

Thus the function $F(N)$ is by no means monotonic on the entire semi-axis and the mapping it gives is not a one-to-one correspondence.

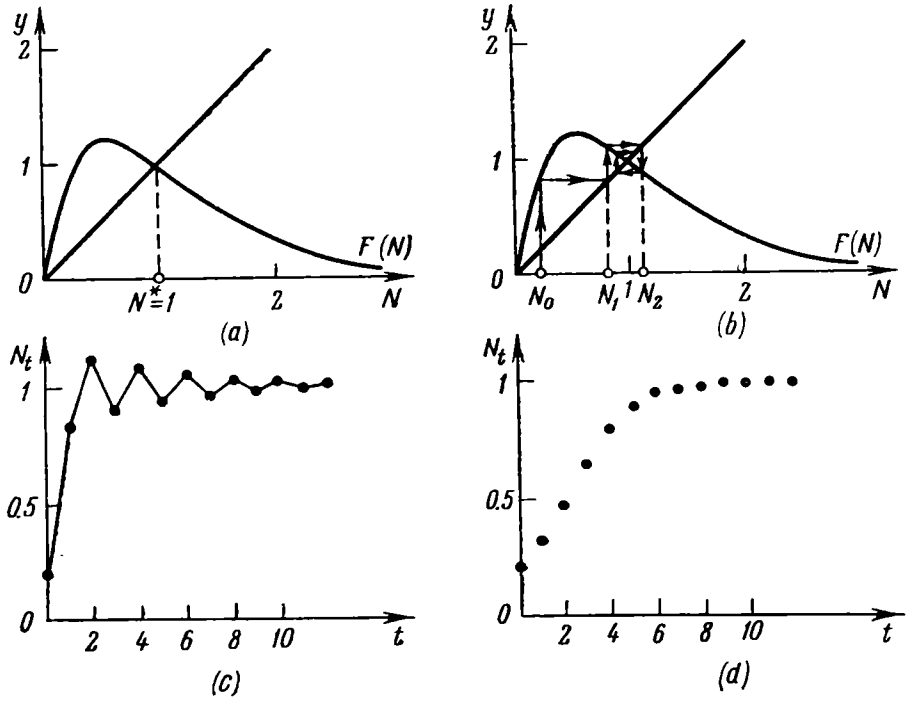

Fig. 5. Equilibrium point for equation (2.6) with $K = 1$, $r = 1.8$: (*a*) equilibrium N^* is found as the intersection point of the curve $y = F(N)$ and the straight line $y = N$ (Lamerey diagram); (*b*) graphic evaluations of the successive values $N_0 = 0.2$, $N_1, N_2, \ldots$ (Lamerey staircase); (*c*) damped oscillations approaching equilibrium; (*d*) a trajectory monotonically approaching N^* ($r = 0.6$).

We can produce a series of concrete $F(N)$ forms describing growth dynamics. So the formal difference analog (we substitute $\Delta N/\Delta t$ for dN/dt, where $\Delta N = N_{t+1} - N_t$ and $\Delta t = 1$) of the logistic equation

$$dN/dt = rN(1 - N/K)$$

becomes

$$N_{t+1} = N_t[1 + r(1 - N_t/K)], \tag{2.5}$$

where parameters r and K are of the same origin as in the logistic equation. However, if at some time N_t exceeds the quantity $K(1 + r)/r$, equation (2.5) yields a negative value of N_{t+1}, which is not the case in the continuous prototype. Hence from this point

of view equation (2.5) is biologically incorrect. The equation

$$N_{t+1} = N_t \exp \{r (1 - N_t/K)\} \tag{2.6}$$

is free from this kind of "incorrectness" and we can regard it as a difference analog of the logistic growth equation. Recently there have been a number of successful attempts to model insect population dynamics *in vivo* and *in vitro* using the three-parameter equation

$$N_{t+1} = N_t\lambda [1 + aN_t]^{-l}, \tag{2.7}$$

where parameters a and b reflect the population self-limiting effects. In various works other forms of equation (2.4) were suggested in connection with population dynamics analysis. We will not list them here but will deal with some general methods of stability analysis for such equations.

The *solution* (or *trajectory*) of equation (2.4) is an arbitrary sequence of values $\{N_t\}$ ($t = 0, 1, 2, \ldots$), which meet the given difference relationship for every t. Obviously, different solutions correspond to different initial values N_0. The stability of the solutions may be defined similarly to Lyapunov's stability for differential equations: for sufficiently small displacements of the initial value the newly obtained solution differs slightly from the original one. Or in formal language, the solution $\{N_t^*\}$ to equation (2.4) we call stable if for every arbitrarily small $\varepsilon > 0$ we can find $\delta(\varepsilon) > 0$ such that $| N_t - N_t^* | < \varepsilon$ for all points of the corresponding trajectories for $t = 1, 2, \ldots, | N_0 - N_0^* | < \delta$.

Similarly, we can extend the definitions of asymptotic stability, of local stability and global, or absolute, stability to include difference equations, however, in the analysis of difference equations there developed somewhat different terminology, which we will touch upon below. The notions introduced will be illustrated by examples of the trajectory behavior for equation (2.6).

If there exists a solution

$$N_t \equiv \text{const} = N^*, \tag{2.8}$$

which we call an *equilibrium*, it must satisfy the equation

$$N^* = F(N^*). \tag{2.9}$$

If the solution (2.8) is stable, we call it a *stable point* (Fig. 5*c*, *d*).

The existence of the equilibrium can be easily found graphically using the so-called "Lamerey diagram" (Fig. 5*a*); the graphic scheme that gives us successive values $N_1, N_2, \ldots$ is known as the "staircase of Lamerey" (Fig. 5*b*).

In the general case the equilibrium is possible if equation (2.9) has at least one positive root N^*. To study the trajectory behavior in the neighbourhood of this equilibrium, we set $N_t = N^* + x_t$, and as in the continuous case we linearize equation (2.4), expanding

F as a power series in $N_t - N^* = x_t$ and truncating the terms of order two and higher. We get

$$x_{t+1} = \left(\frac{dF}{dN}\right)_{N^*} x_t + O(x_t^2). \tag{2.10}$$

It immediately follows from geometric progression convergence that $x_t \to 0$ or $|x_t| \to \infty$ depending on the absolute value of the derivative $(dF/dN)_{N^*}$ being more or less than unity. Thus the equilibrium N^* is stable asymptotically if

$$\left|\left(\frac{dF}{dN}\right)_{N^*}\right| < 1 \tag{2.11}$$

(in this case N^* is the limit point for all sufficiently close trajectories), and unstable if

$$\left|\left(\frac{dF}{dN}\right)_{N^*}\right| > 1. \tag{2.12}$$

The case of

$$\left|\left(\frac{dF}{dN}\right)_{N^*}\right| = 1$$

calls for a further examination of some higher order terms in the expansion (2.10).

In the general case the conditions (2.11) and (2.12) can be made more precise; that is when

$$0 < \left(\frac{dF}{dN}\right)_{N^*} < 1 \tag{2.13}$$

there is a monotonic approach to equilibrium, and when

$$-1 < \left(\frac{dF}{dN}\right)_{N^*} < 0 \tag{2.14}$$

we get damped-stable oscillations around N^*; for

$$\left(\frac{dF}{dN}\right)_{N^*} > 1 \tag{2.15}$$

the displacement from equilibrium monotonically increases and when

$$\left(\frac{dF}{dN}\right)_{N^*} < -1, \tag{2.16}$$

unstable oscillations of increasing amplitude occur around N^*.

Example. For equation (2.6) the equilibrium (2.8) is sought as the solution to

$$\exp\left\{r\left(1 - \frac{N^*}{K}\right)\right\} = 1,$$

whence it follows that there exists a unique equilibrium $N^* = K > 0$ for every r^*. The conditions (2.12) show that the equilibrium is unstable when $r < 0$ or $r > 2$, and it follows from (2.11) that at $0 < r < 2$ there exists a stable point. Or rather, displacements from equilibrium decrease asymptotically when $0 < r < 1$ (Fig. 5*d*) and with oscillations if $1 < r < 2$ (Fig. 5*c*).

The method described enables us to recognize the convergence of the N_t trajectories to equilibrium N^* only for fairly small initial displacements from equilibrium of the initial value N_0. The global character of the trajectory behavior—just as in the case of ordinary differential equations—is defined by finding the corresponding Lyapunov functions. In our example such a function can be presented by

$$V_t = (N_t - K)^2.$$

In fact, V_t has all the necessary attributes of Lyapunov's function:

(1) $V_t \geqslant 0$ and has a minimum $V = 0$ at $N_t = K$;

(2) V_t increment on the trajectory of equation (2.6) is

$$\Delta V_t = V_{t+1} - V_t = (N_{t+1} - N_t)(N_{t+1} + N_t - 2K) =$$
$$= K^2 n_t [\exp\{r(1 - n_t)\} - 1][n_t \exp\{r(1 - n_t)\} + n_t - 2],$$

where

$$n_t = N_t/K.$$

Then the inequality $\Delta V_t \leqslant 0$ reduces to the two systems of inequalities

(a) $e^{r(1-n_t)} \geqslant 1,$

$$e^{r(1-n_t)} + 1 < \frac{2}{n_t};$$

(*b*) $e^{r(1-n_t)} < 1,$

$$e^{r(1-n_t)} + 1 \geqslant \frac{2}{n_t}.$$

The examination of these shows that $\Delta V_t \leqslant 0$ for $0 < r < 2$ and for all $n_t > 0$ while $\Delta V_t = 0$ only for $n_t = N^*/K$. Thus the equilibrium stability is globally asymptotic, i.e. for all initial values $N_0 > 0$ the solution N_t tends to N^*.

2.3. Cycles and "chaos" in solutions to difference equations

A solution $\{N_t^*\}$ to the equation (2.3) made up of a finite set of T values, following in a strict succession (i.e. $N_t^* = N_{t+T}^*$, $t = 0, 1, 2, \ldots$; $N_{t+j}^* \neq N_t^*$, $j = 1, 2, \ldots, T - 1$) we call a *cycle of*

* This is one of the arguments for equation (2.6) to be treated as a difference analog of the logistic equation.

period T (a *T-point cycle* or a *T-cycle*). Figure 6*b* shows a two-point cycle; and Fig. 6*c*, a four-point cycle.

To see whether among solutions to equation (2.3), there are cycles of period, say, $T = 2$ and to calculate these cycles, we should look for a solution such that

$$N_t = N_{t+2} = N_{t+4} = \ldots$$

It is clear that

$$N_{t+2} = F(N_{t+1}) = F[F(N_t)] = F^{(2)}(N_t).$$

If we consider the sequence $\{N_t\}$ with a step of 2, the equation

$$N_{t+2} = F^{(2)}(N_t) \tag{2.17}$$

again is a first order difference equation and to examine it we shall use the above method.

A cycle of period 2 is possible if there exist two different positive roots N_1^2 and N_2^2 for the system of equations

$$N_2 = F(N_1), \quad N_1 = F(N_2). \tag{2.18}$$

Obviously we can find them among the solutions to the equation

$$N = F^{(2)}(N).$$

Figure 6*a* illustrates the situation.

Linearizing the equation (2.17) at a point, for instance at N_2^2, and checking the condition (2.11), which in this case has the form

$$\left|\left(\frac{dF^{(2)}}{dN}\right)_{N_2^2}\right| < 1,$$

we can see whether N_2^2 is a limit point for sufficiently close trajectories of equation (2.3). By the rule of composite function differentiation and (2.18), we have

$$\left(\frac{dF^{(2)}}{dN}\right)_{N_2^2} = \left(\frac{dF}{dN}\right)_{F(N_2^2)}\left(\frac{dF}{dN}\right)_{N_2^2} = \left(\frac{dF}{dN}\right)_{N_1^2}\left(\frac{dF}{dN}\right)_{N_2^2}.$$

We easily see that the derivative $dF^{(2)}/dN$ at the other point of the cycle, N_1^2, is the same, that is

$$\left(\frac{dF^{(2)}}{dN}\right)_{N_1^2} = \left(\frac{dF^{(2)}}{dN}\right)_{N_2^2} = \prod_{j=1}^{2}\left(\frac{dF}{dN}\right)_{N_j^2}.$$

Thus both cycle points simultaneously do, or do not, give limit points to the trajectories of the equation.

Similarly, when studying the stability of a T-cycle with values $(N_1^T, N_2^T, \ldots, N_T^T)$ we will be interested in the derivative

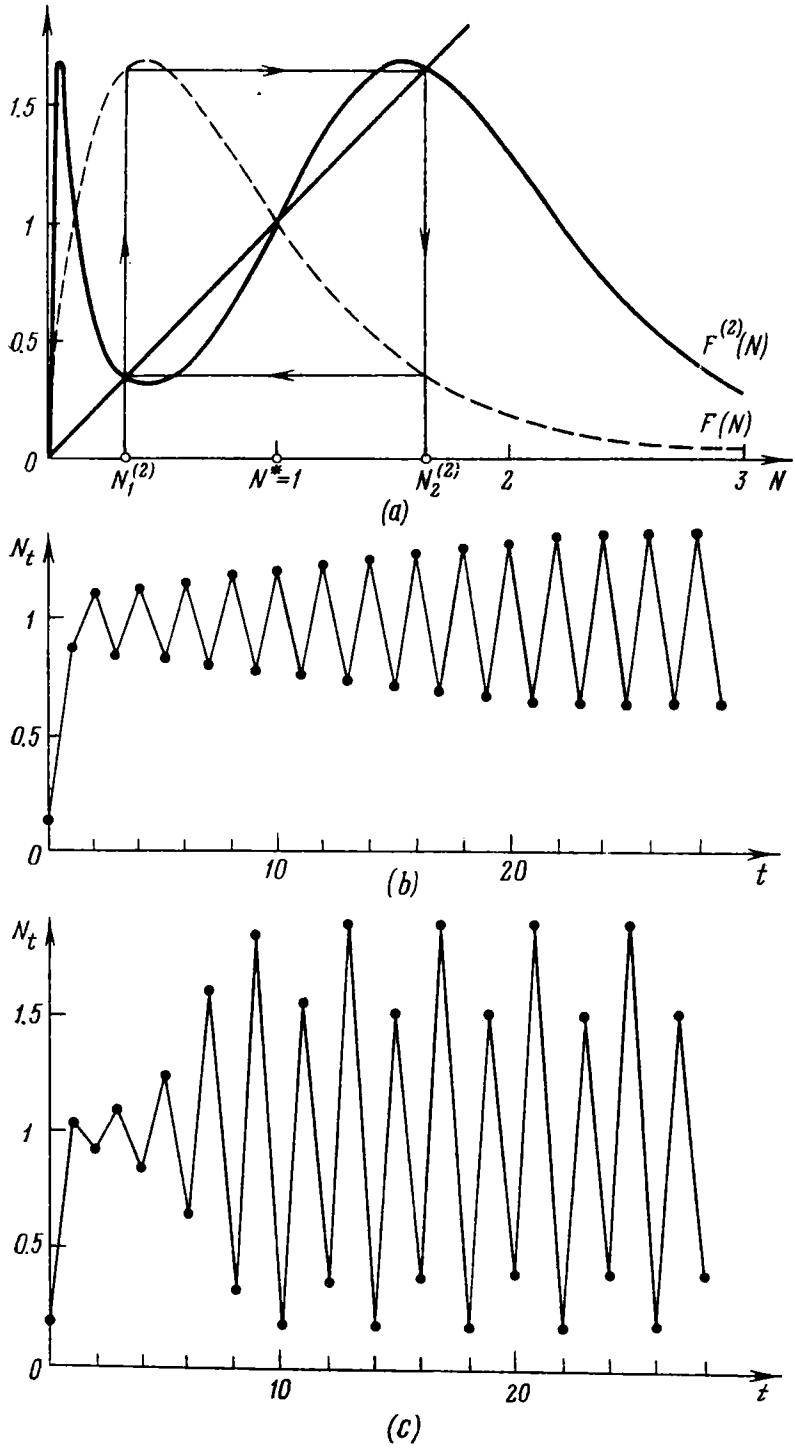

Fig. 6. Cyclic behavior of solutions to (2.6): (*a*) Lamerey diagram for a two-point cycle ($r = 2.4$); (*b*) 2-cycle ($r = 2.1$; $N_0 = 0.15$); (*c*) 4-cycle ($r = 2.6$; $N_0 = 0.1$).

$dF^{(T)}/dN$ at these points of the cycle. So for point N_1^T we get

$$\left(\frac{dF^{(T)}}{dN}\right)_{N_1^T}=\left(\frac{dF}{dN}\right)_{F^{(T-1)}(N_1^T)}\left(\frac{dF^{(T-1)}}{dN}\right)_{N_1^T}=\cdots$$

$$\cdots=\left(\frac{dF}{dN}\right)_{N_T^T}\left(\frac{dF}{dN}\right)_{N_{T-1}^T}\cdots\left(\frac{dF}{dN}\right)_{N_1^T}.$$

The values of the derivative at all the other cycle points coincide with the expression obtained to the order of factors; consequently, all of them are the same and equal to

$$\lambda^{(T)}=\prod_{j=1}^{T}\left(\frac{dF}{dN}\right)_{N_j^T}, \tag{2.19}$$

so that all the T-cycle points either simultaneously serve as limit points for the trajectories of the equation or fail to do so. This fact justified the following terminology.

A cycle $(N_1^T, \ldots, N_T^T)$ is called *attracting*, *repulsing* or *neutral* if, respectively,

$$\lambda^{(T)}=\prod_{j=1}^{T}\left(\frac{dF}{dN}\right)_{N_j^T}<1, \tag{2.20}$$

$$\lambda^{(T)}>1 \tag{2.21}$$

or

$$\lambda^{(T)}=1. \tag{2.22}$$

Obviously the introduced definitions are similar to asymptotic stability, instability, and non-asymptotic stability, respectively.

Example. For equation (2.6)

$$F^{(2)}(N)=\exp\left\{r\left(2-\frac{N}{K}\left[\exp\left\{r\left(1-\frac{N}{K}\right)+1\right\}\right]\right)\right\},$$

and according to (2.18)

$$\frac{N}{K}\left[\exp\left\{r\left(1-\frac{N}{K}\right)\right\}+1\right]=2,$$

which on substituting

$$N=K(1+x)$$

gives

$$x=\tanh\left(\frac{1}{2}rx\right), \tag{2.23}$$

where

$$\tanh x=\frac{e^x-e^{-x}}{e^x+e^{-x}}.$$

The number of roots of the transcendental equation (2.23) is derived from graphic analysis (Fig. 7). For $r < 2$ there is only one solution $x = 0$ (i. e. $N^* = K$), which is that of the globally stable equilib-

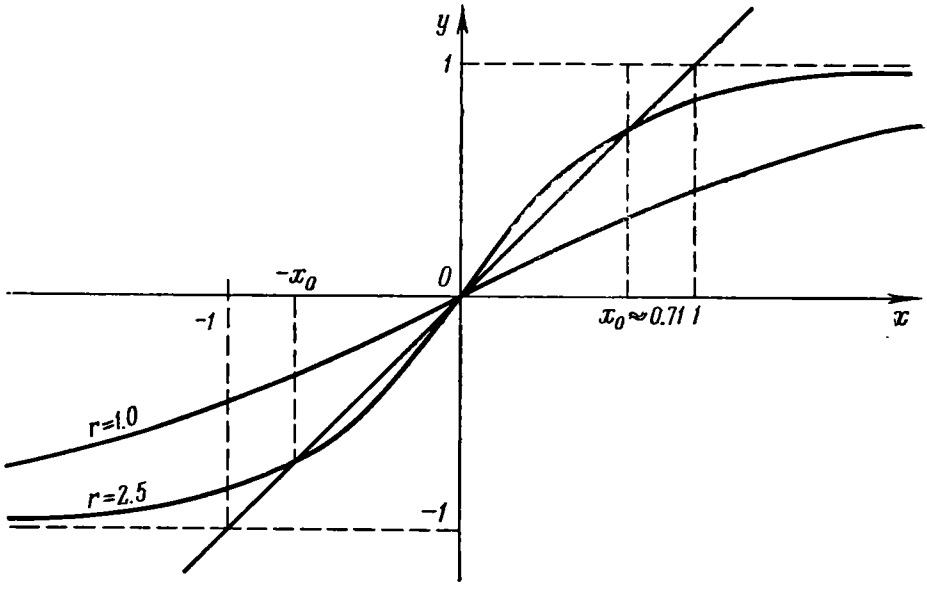

Fig. 7. Graphic solution of equation (2.23): the solution x_0 is found as the x-coordinate of the intersection point of the line $y = x$ and the curve $y = \tanh(rx/2)$; the tangent slope at $x = 0$ is $r/2$.

rium we have found before. For $r > 2$ the straight line $y = x$ intersects the curve $y = \tanh\left(\frac{1}{2}rx\right)$ at three points: $x = 0$ and $x = \pm x_0$ where $0 < x_0 < 1$. Checking the conditions (2.12) and (2.20) shows that for $r > 2$ the solution $x = 0$ ($N^* = K$) is unstable, while the points

$$N^2_{1,2} = K(1 \pm x_0) \tag{2.24}$$

make up an attracting 2-cycle, when

$$0 < r[2 - r(1 - x_0^2)] < 2.$$

This condition assigns the interval of values

$$2 < r < r_2 \approx 2.526, \tag{2.25}$$

for which the points $N^2_{1,2}$ form an attracting cycle. Since the equilibrium $N^* = K$ is unstable in this case, it follows that trajectories (2.6) originating in the vicinity of $N^2_{1,2}$ approach these points, that is a stable cycle of period 2 is realized. Strictly speaking, there is no global stability of the cycle (N^2_1, N^2_2), if only because the solution $N_t = N^* = K$ never approaches it. However, numerous computa-

tions show that almost for all initial values N_0 subject to conditions (2.25) the trajectories approach the cycle (N_1^2, N_2^2).

When the parameter r increases further, stable cycles of period 4, 8, 16, . . ., 2^k (k is any positive integer) may be encountered.

A more thorough investigation of the behavior of trajectories of (2.6) for a varying parameter r calls for more sophisticated mathematics, namely that of dynamic systems theory and bifurcation theory.

Recently such a study has been undertaken. The results suggest in particular that:

(1) for every fixed $r > 0$ among all the solutions there can be no more than one attracting cycle;

(2) if there is an attracting cycle of period n, the trajectories for almost all initial values approach this cycle;

(3) if the population behavior described by (2.3) differs in a way from the population dynamics given by (2.6) and having an attracting cycle, but is similar to it (in some sense), the asymptotic behavior of trajectories of both populations will be the same, i.e. (2.3) will also have an attracting cycle;

(4) for every n there exists such $r = r(n)$, that (2.6) has an attracting cycle of period n;

(5) for r increasing within a bounded interval $(0, r_0)$ the solutions bifurcate: cycles of period 2^k are replaced by 2^{k+1}-cycles ($k = 0, 1, 2, \ldots$).

Notice that such a detailed analytical study of the solution behavior patterns is not of theoretical interest only. The point is that when we calculate the trajectory of a difference equation on a computer, because of the limited word length the results $\{\hat{N}_t\}$ will be somewhat different from the real trajectory $\{N_t\}$. Obviously, a computer allows only a finite—though very large—number of different $\hat{N}_t$ values, namely 2^m, where m is the number of digits in the word. Accordingly, after a fairly long period of time, at t, we will inevitably get a value N_{t-T} we have already had before, i.e. the sequence $\{\hat{N}_t\}$ will be periodic—with a sufficiently big period T—no matter whether or not the real trajectory $\{N_t\}$ was periodic. The examination of the equations enables us to establish the extent to which the calculated sequence $\{\hat{N}_t\}$ reflects the behavior of the real trajectory $\{N_t\}$.

Apart from equilibrium and cycles solutions of the difference equation can have another form of behavior. It is the so-called *chaotic* trajectories, that is non-periodic sequences $\{N_t\}$ which even do not approach any attracter (equilibrium or a cycle). It turns out that there is a connection between the presence of 3-point cycles and the existence of chaotic solutions. A theorem of general character is proved here. It states that if equation (2.3) has a 3-point cycle, it also has solutions of any period n, and what is more, there exists an

uncountable set of initial values N_0, for which the solutions do not approach any of these cycles, i.e. show a chaotic behavior. Thus the

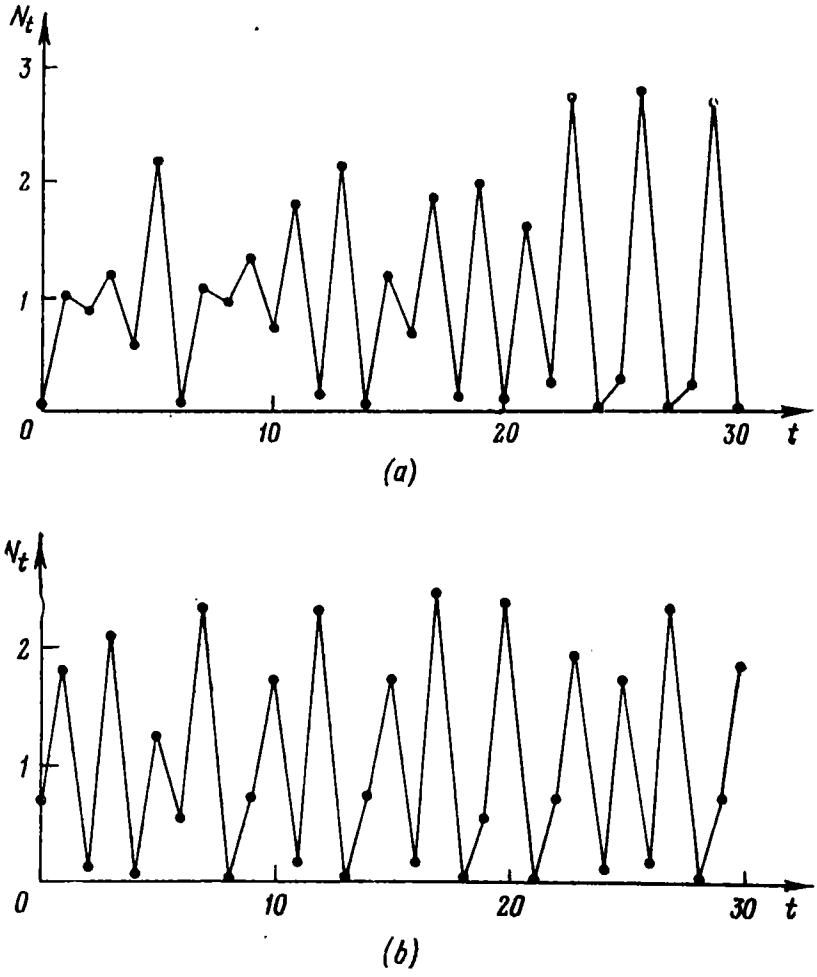

Fig. 8. Chaotic behavior (2.23) for $r = 3.2$ ($K = 1$): (*a*) $N_0 = 0.05$; divergent oscillations about the unstable equilibrium $N^* = 1$, starting from $t = 23$ fall into the neighborhood of a 3-cycle. Since this cycle is unstable, later the trajectory behavior will necessarily change; (*b*) $N_0 = 0.7$; a chaotic trajectory with no apparent "pattern".

behavior of the solution to such a system radically depends on the initial value N_0.

Example. In the case of equation (2.6) we solve for a 3-point cycle as follows

$$N_1 = aK,$$

$$N_2 = bK,$$

$$N_3 = cK, \quad \text{where } (0 < a < b < c),$$

whence a, b, and c are to satisfy the system

$$b = a \exp \{r(1-a)\},$$
$$c = b \exp \{r(1-b)\}, \tag{2.26}$$
$$a = c \exp \{r(1-c)\}.$$

Taking the logarithm of these equations and adding term by term we get the relationship

$$a + b + c = 3,$$

using which we can show that a is the smallest positive root of the transcendental equation

$$\ln\left[\frac{3}{a} - 1 - \exp\{r(1-a)\}\right] = r[2 - a - a\exp\{r(1-a)\}]. \tag{2.27}$$

Graphic analysis of (2.27) indicates that for $r > r_c \approx 3.102$ there exist 2 different 3-point cycles, while for $r < r_c$ there are no 3-point cycles at all. Thus according to the above general statement, the solutions of (2.6) produce a chaotic behavior when $r > r_c$ (Fig. 8).

Thus using only one equation (2.6) as an example we could convincingly demonstrate all the variety of solutions of difference equations. The rich behavior spectrum contains a stable equilibrium, stable cycles of any period and also a chaotic state dominated by the initial conditions. Perhaps the success in application of difference equations to natural population modelling can be somehow explained by this rich dynamic behavior of model trajectories.

2.4. Discrete model of population age structure

The equations in previous models of population dynamics described the variations only of the total population number $N(t)$, and no assumptions were made about the relationships between the specimens age and their mortality and natality. However in many cases the population age structure is of significance.

In a life cycle of any organism we can find either a number of phases of development, like for instance in insects, or several age periods, defined in some time units, for example in years from birth of a mammal. Then the population naturally splits into a number n of age groups. The way in which we divide the population into age groups is generally determined by the biological peculiarities of the organisms and the specific features of the problem considered. The simplest assumptions about the relationships between age groups lead to the so-called *Leslie model.*

Let $x_i(t)$ denote the number of the ith age group ($i = 1, 2, \ldots, n$) when sex distinctions are not taken into account, and the number of females in the ith group, if the distinctions are significant for the

population considered. The time t counts down the discrete moments of transfer from one age group to the next one. Suppose the natality functions $b_i(x_1, \ldots, x_n)$ indicating the offspring numbers (or number of the new-born females) in the ith age group, are represented by linear functions of the numbers in the given age group only

$$b_i(x_1, \ldots, x_n) = b_i x_i, \quad i = 1, 2, \ldots, n, \tag{2.28}$$

with non-negative natality coefficients b_i. Then the number of the first age group made up of the offsprings from all other age groups can be given by

$$x_1(t+1) = \sum_{i=1}^{u} b_i x_i(t). \tag{2.29}$$

Suppose the functions $s_i(x_1, \ldots, x_n)$ describe the transfer from the ith age group to the $(i+1)$th group and they are also linear functions of only the numbers in the ith group:

$$s_i(x_1, \ldots, x_n) = s_i x_i, \qquad i = 1, 2, \ldots, n-1 \tag{2.30}$$

where the survival coefficients s_i $(0 < s_i \leqslant 1)$ show the fraction of the ith group organisms that live to the $(i+1)$th age. Then for all the groups, starting from the second, we have the relationship

$$x_{i+1}(t+1) = s_i x_i(t), \quad i = 1, 2, \ldots, n-1. \tag{2.31}$$

Assumptions (2.28) and (2.30) mean that we do not take into account the parameter variations induced by the environmental properties and neglect the overall population effect on natality and mortality.

If we denote by $\mathbf{x}(t)$ the column vector built up of the numbers of all age groups, it follows from (2.29) and (2.31) that

$$\mathbf{x}(t+1) = L\mathbf{x}(t), \tag{2.32}$$

where the $(n \times n)$ square matrix L has the form

$$L = \begin{Vmatrix} b_1 & b_2 & \ldots & b_{n-1} & b_n \\ s_1 & 0 & & & 0 \\ & s_2 & 0 & & \\ & & \ddots & \ddots & \\ 0 & & & s_{n-1} & 0 \end{Vmatrix},$$

where $b_i \geqslant 0$, $i = 1, 2, \ldots, n$;

$$0 < s_j \leqslant 1, \qquad j = 1, 2, \ldots, n-1 \tag{2.33}$$

and is known as the *Leslie matrix*.

Equation (2.32) represents a system of n first-order linear difference equations with constant coefficients. The solution, correspond-

ing to the initial number distribution x (0), can be written as

$$\mathbf{x}(t) = L^t \mathbf{x}(0), \qquad t = 1, 2, \ldots,$$

where L^t is the degree of matrix L.

Matrix L defines a linear operator in an n-dimensional Euclidean space, and this operator is also named the *Leslie operator*. Because the variables $x_i(t)$ stand for population numbers, they are non-negative, and we will be concerned with the Leslie operator action in the positive orthant P^n of the n-dimensional space. Since all the

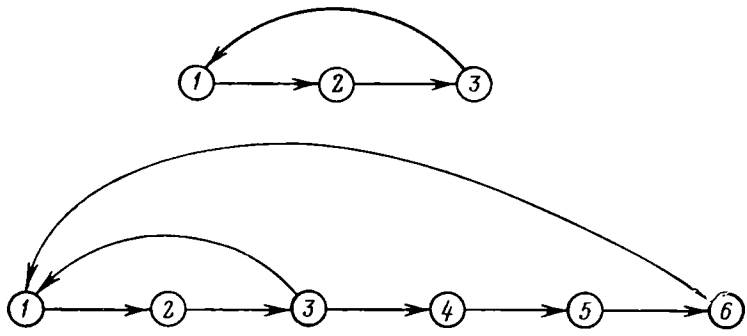

Fig. 9. Examples of graphs belonging to Leslie matrices. The link $n \to 1$ provides strong connectedness of the graph.

elements of matrix L are non-negative (hence the matrix itself is called *non-negative*), it is clear that any vector of the positive orthant cannot be brought beyond its boundaries by the Leslie operator, that is the trajectory x (t) $(t = 1, 2, \ldots)$ remains within P^n. All the subsequent Leslie model properties follow from the non-negativity of the matrix L and its specific structure.

The asymptotic behavior of solutions to equation (2.32) is essentially bound up with spectral properties of matrix L, with the most essential ones being given by the well-known Perron-Frobenius theorem. To use this theorem we should be convinced that the non-negative matrix L is *indecomposable*, that is no permutation of rows and corresponding columns in L can yield the form

$$\begin{Vmatrix} A & 0 \\ C & B \end{Vmatrix}$$

where A and B are square blocks. The notion of matrix indecomposability can also be formulated in terms of graphs, which represent the location of non-zero matrix elements. Such a graph has n vertices and each non-zero matrix element with indices (i, j) is presented by a link between vertices i and j with the direction $j \to i$. Thus graphs in Fig. 9 correspond to matrices on page 64.

We call a graph *strongly connected* if for each pair of vertices k and l there exists a directed path from k to l. It can be shown that matrix indecomposability is equivalent to strong connectedness of an appropriate graph. It follows that for a Leslie matrix to the indecomposable it is necessary and sufficient that

$$b_n \neq 0. \tag{2.34}$$

This condition corresponds to n being not the maximal possible but the most fertile age of specimens. It is clear that numbers in postfertile groups can influence the age structure of younger groups only if limiting effects of overall population numbers are involved. Since the Leslie model does not account for effects of this kind, constraint (2.34) seems quite reasonable, that is we can take into consideration fertile groups alone. If the numbers in postfertile groups are still of some interest, they can very easily be found at any time from the dynamics, of the last fertile group $x_n(t)$:

$$x_{n+1}(t+1) = s_n x_n(t)$$

$$x_{n+2}(t+1) = s_{n+1} x_{n+1}(t)$$

$$\cdots\cdots\cdots\cdots\cdots\cdots$$

$$x_{n+k}(t+1) = s_{n+k-1} x_{n+k-1}(t),$$

or substituting

$$x_{n+j}(t) = s_n s_{n-1} \ldots s_{n+j-1} x_n(t-j), \qquad j = 1, 2, \ldots, k$$

(k is the number of postfertile age groups). Therefore, in what follows we will only examine indecomposable Leslie matrices of the order equal to the number of the last fertile group. Expanding the characteristic determinant of matrix (2.33), by the elements of the first row or in some other way, we can get the characteristic equation

$$p(\lambda) = \det(\lambda I - L) =$$
$$= \lambda^n - b_1\lambda^{n-1} - b_2 s_1 \lambda^{n-2} - \ldots - b_n s_1 \ldots s_{n-1} = 0. \tag{2.35}$$

Since $b_n \neq 0$, the free term in (2.35) is non-zero, too, consequently, the equation has no zero roots, that is matrix L is non-singular.

2.5. Spectral properties of Leslie operator

As said before, Leslie model solutions mostly behave according to the spectral properties of matrix L or the corresponding operator L.

Consider the case where operator L has *simple structure*, that is, it has n linearly independent eigenvectors. Since eigenvectors corresponding to different eigenvalues are linearly independent, simple structure occurs when all the operator eigenvalues are different. In general, this is not a necessary condition: there exist linear operators of simple structure with multiple roots of their characteristic polynomials. However, for a Leslie operator it can be shown that unit

multiplicity of all eigenvalues is a necessary and sufficient condition of simple structure.

In fact, the general criterion of simple structure for a linear operator A is the linearity of all prime divisors of the matrix A minimal polynomial. We refer the *minimal polynomial* of matrix A to the nullifying polynomial of the minimal degree for this matrix

$$\psi(A) = 0$$

(with the leading coefficient equal to unity). It has been known* that

$$\psi(\lambda) = D_n(\lambda)/D_{n-1}(\lambda), \tag{2.36}$$

where $D_k(\lambda)$ is the greatest common divisor for k-order minors of the characteristic matrix $\lambda I - L$ (the coefficient for the highest degree in λ is taken to be unitary). The minor of the given matrix, built for the last $n-1$ rows and first $n-1$ columns has the form

$$(\lambda I - L)\begin{pmatrix} 2, & 3, & \ldots, & n \\ 1, & 2, & \ldots, & n-1 \end{pmatrix} = (-1)^{n-1} s_1 s_2 \ldots s_{n-1} \tag{2.37}$$

with no λ entries, hence $D_{n-1}(\lambda) = 1$, then $D_k(\lambda) = 1$, $k = n-2, \ldots, 1$. It follows in particular that

$$\psi(\lambda) = D_n(\lambda), \tag{2.38}$$

that is Leslie matrix minimal polynomial coincides with the characteristic one. Its elementary divisors in the field of complex numbers are the degrees of binomials $(\lambda - \lambda_j)$, where λ_j are different eigenvalues of L. For all of them to be of degree one it is necessary and sufficient for all n eigenvalues to be different.

Thus the Leslie operator has simple structure if and only if all its eigenvalues are different.

From (2.38) we can derive some other statements about the operator L. The fact that dimensionality of the L minimal polynomial coincides with that of the space itself, means that the space is cyclic with respect to this operator, i.e. there exists a vector $\mathbf{e}$, such that vectors $\mathbf{e}$, $L\mathbf{e}$, $L^2\mathbf{e}$, $\ldots$, $L^{n-1}\mathbf{e}$ are linearly independent and the vector $L^n\mathbf{e}$ is their linear combination. For instance, $\mathbf{e} = (1, 0, \ldots, 0)$ can be such a vector.

Invariant polynomials, that is polynomials

$$i_1(\lambda) = \psi(\lambda) = \frac{D_n(\lambda)}{D_{n-1}(\lambda)}, \qquad i_2(\lambda) = \frac{D_{n-1}(\lambda)}{D_{n-2}(\lambda)}, \ \ldots, \qquad i_n(\lambda) = \frac{D_1(\lambda)}{D_0(\lambda)} \tag{2.39}$$

($D_0(\lambda) \equiv 1$ by definition), for the Leslie matrix have the form

$$i_1(\lambda) = \psi(\lambda) = D_n(\lambda), \qquad i_2(\lambda) = 1, \ \ldots, \ i_n(\lambda) = 1 \tag{2.40}$$

* Gantmacher F. R., *The Theory of Matrices*, Chelsea, New York, 1960.

A normal Jordan form for any matrix represents the decomposition of space into cyclic subspaces, corresponding to the elementary divisors of all the invariant polynomials. This and the equalities (2.40) enables one to state that if the Leslie matrix spectrum consists of m different values λ_j ($j = 1, 2, \ldots, m \leqslant n$) with multiplicities k_j ($k_1 + k_2 + \ldots + k_m = n$), the normal Jordan form for this matrix has exactly m blocks of $k_j \times k_j$ size and numbers λ_j on the main diagonal. Therefore equal eigenvalues are gathered in one and the same Jordan block.

Thus, a Leslie matrix can be represented in the form

$$L = P\,\{J_1, J_2, \ldots, J_m\}\,P^{-1}, \tag{2.41}$$

where J_j is a $k_j \times k_j$ Jordan block

$$J_j = \begin{Vmatrix} \lambda_j & 1 & & 0 \\ & \lambda_j & \ddots & \\ & & \ddots & 1 \\ 0 & & & \lambda_j \end{Vmatrix}. \tag{2.42}$$

If all the eigenvalues λ_j are different, the columns of the transforming matrix P are made of eigenvectors corresponding to different eigenvalues. Generally these are the vectors which form the so-called Jordan basis. Because all the equal eigenvalues are gathered in one and the same Jordan block, vectors $\mathbf{e}_1, \mathbf{e}_2, \ldots, \mathbf{e}_k$ of this basis, corresponding to the eigenvalue λ of multiplicity k, may be successively obtained from the relationships

$$(L - \lambda I)\,\mathbf{e}_1 = 0, \qquad (L - \lambda I)\,\mathbf{e}_2 = \mathbf{e}_1, \ldots,$$
$$(L - \lambda I)\,\mathbf{e}_k = \mathbf{e}_{k-1}. \tag{2.43}$$

An arbitrary function of a matrix and, in particular, any natural degree t of a matrix, is defined by its values for the spectrum. Evidently

$$L^t = P\,\{J_1^t, J_2^t, \ldots, J_m^t\}\,P^{-1} \tag{2.44}$$

where the degree of a Jordan $k \times k$ block corresponding to the eigenvalue λ of multiplicity k for a sufficiently long t has the form

$$J^t(\lambda) = \begin{Vmatrix} \lambda^t & \frac{t}{1!}\lambda^{t-1} & \frac{t(t-1)}{2!}\lambda^{t-2} & \ldots & \frac{t(t-1)\ldots(t-k+2)}{(k-1)!}\lambda^{t-k+1} \\ 0 & \lambda^t & \frac{t}{1!}\lambda^{t-1} & \ldots & \frac{t(t-1)\ldots(t-k+3)}{(k-2)!}\lambda^{t-k+2} \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ & & & & \frac{t}{1!}\lambda^{t-1} \\ 0 & 0 & 0 & \ldots & \lambda^t \end{Vmatrix}. \tag{2.45}$$

When all the eigenvalues λ_j are different, formulas (2.44) and (2.45) are reduced to

$$L^t = P \begin{vmatrix} \lambda_1^t & & & 0 \\ & \lambda_2^t & & \\ & & \ddots & \\ 0 & & & \lambda_n^t \end{vmatrix} P^{-1}. \tag{2.46}$$

With formulas (2.44)-(2.45) we can calculate the age distribution $\mathbf{x}(t)$ at any step t and for any initial distribution $\mathbf{x}(0)$, study the asymptotic behavior of the system trajectories as $t \to \infty$, that is evaluate the limit

$$\lim_{t\to\infty} L^t \mathbf{x}(0). \tag{2.47}$$

From (2.45) it is obvious that if $|\lambda_j| < 1$ for all λ_j then

$$\lim_{t\to\infty} L^t \mathbf{x}(0) = 0.$$

If there exists such a λ_j that $|\lambda_j| > 1$ then

$$\lim_{t\to\infty} L^t \mathbf{x}(0) = \infty.$$

Thus a non-trivial limit in (2.47) can exist only if the maximal absolute eigenvalue equals unity. In both previous cases it would be more interesting to look at the limit

$$\lim_{t\to\infty} \frac{L^t \mathbf{x}(0)}{\lambda_1^t}, \tag{2.48}$$

where λ_1 is the eigenvalue with the largest absolute value.

The Perron-Frobenius theorem states for non-negative indecomposable matrices A*:

(1) A has a real positive eigenvalue r (the largest eigenvalue), which is a prime solution to the characteristic equation. If λ_j is any other eigenvalue for A, then $|\lambda_j| \leqslant r$.

(2) There exists a positive eigenvector corresponding to r.

(3) If A has h eigenvalues with their absolute values equal to r, then all of them are different and they present the solutions to the equation $\lambda^h - r^h = 0$; h is known as *index of imprimitivity*** of the matrix A.

(4) If $\lambda_1, \lambda_2, \ldots, \lambda_n$ is the set of all eigenvalues of matrix A and $\theta = \exp(i2\pi/h)$, then $\lambda_1\theta, \ldots, \lambda_n\theta$ coincides up to the order with $\lambda_1, \ldots, \lambda_n$.

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* See, for instance, Marcus M., Minc H. *A Survey of Matrix Theory and Matrix Inequalities*, Allyn and Bacon, Boston, 1964.

** The matrix is called *primitive* when $h = 1$.

A Leslie matrix with $b_n \neq 0$ is indecomposable and, consequently, has the largest eigenvalue $r > 0$, which is a prime root to the characteristic polynomial (2.35). Notice that by the signs rule of Decartes r is also the only positive root of this polynomial, since among its coefficients sign only changes once.

Are there any other eigenvalues with the absolute value equal to r? We know that the imprimitivity index of a matrix equals the greatest common divisor for

$$n - n_1, \qquad n_1 - n_2, \ldots, n_{q-1} - n_q,$$

where $n > n_1 > \ldots > n_q$ are the degrees of all non-zero terms in the characteristic polynomial*. In the polynomial (2.35) the coefficient at λ^m $(0 \leqslant m < n)$ is different from zero if $b_{n-m} \neq 0$. Denote by $i_1 < i_2 < \ldots < i_q$ the numbers of all age groups with non-zero natalities, or in other words, the indices of all $b_j \neq 0$. Notice that $i_q = n$ follows from indecomposability. From (2.35) we find

$$n_{i_s} = n - i_s, \qquad s = 1, 2, \ldots, q,$$

whence

$$h(L) = \text{GCD}\ \{n - (n - i_1), (n - i_1) - (n - i_2), \ldots$$
$$\ldots, (n - i_{q-1}) - (n - i_q)\} =$$
$$= \text{GCD}\ \{i_1, i_2 - i_1, \ldots, i_q - i_{q-1}\} = \text{GCD}\ \{i_1, i_2, \ldots, i_q\}.$$

Thus the imprimitivity index for a Leslie matrix is given by the greatest common divisor for the numbers of the age groups with non-zero natality. In particular, for a Leslie matrix to be primitive it is sufficient either for b_1 to be positive, or for some two successive groups to be fertile, that is there should exist such a j that $b_j \neq 0$ and $b_{j+1} \neq 0$.

Since the Jordan form is defined within the order of blocks, L can be presented in the form

$$L = P\ \{\lambda_1, \lambda_2, \ldots, \lambda_h, J_{h+1}, \ldots, J_m\}\ P^{-1}, \tag{2.49}$$

where $\lambda_1 = r, \lambda_2, \ldots, \lambda_h$ are the h eigenvalues with the absolute values equal to r. It follows from the relationships $LP = PJ$ and $P^{-1}L = JP^{-1}$ that the first h columns of matrix P and the first h rows of matrix P^{-1} are, up to a coefficient, the characteristic column vectors and the characteristic row vectors, respectively, corresponding to the eigenvalues $\lambda_1, \lambda_2, \ldots, \lambda_h$.

If $\mathbf{C}(\lambda)$ stands for the characteristic column vector and $\mathbf{R}(\lambda)$ for the characteristic row vector, both corresponding to λ, it can be

* Gantmacher, F. R., *The Theory of Matrices*, Chelsea, New York, 1960.

shown that

$$\mathbf{C}(\lambda) = \sqrt{\frac{r^{n-1}}{p'(r)}}\left[\frac{c_1}{1}, \frac{c_2}{\lambda}, \ldots, \frac{c_n}{\lambda^{n-1}}\right]^T \tag{2.50}$$

$$\mathbf{R}(\lambda) = \sqrt{\frac{r^{n-1}}{p'(r)}}\left[\frac{q_1(\lambda)}{c_1\lambda^n}, \frac{q_2(\lambda)}{c_2\lambda^{n-1}}, \ldots, \frac{q_n(\lambda)}{c_n\lambda}\right], \tag{2.51}$$

where

$$c_i = \begin{cases} 1, & \text{if } i=1, \\ s_1 s_2 \ldots s_{i-1}, & \text{if } i=2, \ldots, n, \end{cases}$$

$q_i(\lambda)$ are "segments" of the characteristic polynomial $p(\lambda)$:

$$q_i(\lambda) = \sum_{j=i}^{n} b_j c_j \lambda^{n-j}.$$

For any complex z we have

$$\sum_{i=1}^{n} q_i(z) = zp'(z) - np(z),$$

and hence for $z = r$

$$p'(r) = \frac{1}{r}\sum_{i=1}^{n} q_i(r) > 0.$$

The structure of vectors (2.50) and (2.51) and the real coefficient we find there provide the following conditions for the scalar products:

$$[\mathbf{C}(\lambda_i), \mathbf{R}(\lambda_i)] = 1, \qquad [\mathbf{C}(\lambda_i), \mathbf{R}(\lambda_j)] = 0, \qquad i \neq j;\ i, j = 1, 2, \ldots, h. \tag{2.52}$$

Therefore the first h columns of matrix P and the first h rows of P^{-1} in the expression (2.52) are respectively $\mathbf{C}(\lambda_1)$, $\mathbf{C}(\lambda_2)$, ..., $\mathbf{C}(\lambda_h)$ and $\mathbf{R}(\lambda_1)$, $\mathbf{R}(\lambda_2)$, ..., $\mathbf{R}(\lambda_h)$.

Since

$$|\lambda_{h+1}| < r, \ldots, |\lambda_n| < r,$$

it follows from (2.45) that for the corresponding Jordan blocks we have

$$\lim_{t\to\infty} \frac{J_j^t}{r^t} = 0, \qquad j = h+1, \ldots, m.$$

Moreover, the Perron-Frobenius theorem gives

$$\frac{\lambda_l}{r} = \cos\frac{2\pi l}{h} + i\sin\frac{2\pi l}{h} = \varepsilon^{l-1}, \qquad l = 1, 2, \ldots, h,$$

where

$$\varepsilon = \cos\frac{2\pi}{h} + i\ \sin\frac{2\pi}{h} = e^{i2\pi/h}$$

is a primitive hth root of unity.

Now for the limit in (2.48) at $\lambda_1 = r$ we get

$$\lim_{t\to\infty}\frac{L^t\mathbf{x}}{r^t} = \lim_{t\to\infty} P\,\mathrm{diag}\{1,\ \varepsilon^t,\ \varepsilon^{2t},\ \ldots,\ \varepsilon^{(h-1)t},\ 0,\ \ldots,\ 0\}\,P^{-1}\mathbf{x}$$

$$= \lim_{t\to\infty}\mathscr{L}(\mathbf{x},\ t) \qquad (2.53)$$

with the rate of approach, following (2.45), defined by

$$\frac{t^{k-1}}{r^{k-1}(k-1)!}\left|\frac{\lambda_{h+1}}{r}\right|^{t-k+1},$$

where λ_{h+1} is the second largest in its absolute value eigenvalue for L, and k is its multiplicity.

To simplify we denote

$$\mathbf{C}(\lambda_l) = \mathbf{C}_l, \qquad \mathbf{R}(\lambda_l) = \mathbf{R}_l, \qquad l = 1,\ 2,\ \ldots,\ h.$$

Rearranging the limit vector function we have

$$\mathscr{L}(\mathbf{x},\ t) = P\begin{Vmatrix}\mathbf{R}_1\\ \varepsilon^t\mathbf{R}_2\\ \cdot\\ \cdot\\ \cdot\\ \varepsilon^{(h-1)}\mathbf{R}_h\\ 0\\ \cdot\\ \cdot\\ \cdot\\ 0\end{Vmatrix}\mathbf{x} = \|\,\mathbf{C}_1\mathbf{C}_2\ \ldots\ \mathbf{C}_h\ \ldots\,\|\begin{bmatrix}(\mathbf{R}_1,\ \mathbf{x})\\ \varepsilon^t(\mathbf{R}_2,\ \mathbf{x})\\ \cdot\\ \cdot\\ \cdot\\ \varepsilon^{(h-1)}(\mathbf{R}_h,\ \mathbf{x})\\ 0\\ \cdot\\ \cdot\\ \cdot\\ 0\end{bmatrix}$$

$$= \sum_{l=1}^{h}\varepsilon^{(l-1)t}(\mathbf{R}_l,\ \mathbf{x})\,\mathbf{C}_l. \qquad (2.54)$$

On substituting (2.50) and (2.51) the ith component of $\mathscr{L}(\mathbf{x},\ t)$ takes the form

$$\mathscr{L}_i(\mathbf{x},\ t) = \frac{c_i}{p'(r)\,r^i}\sum_{k=1}^{n}\frac{q_k(r)\,r^{k-1}x_k}{c_k}\sum_{l=0}^{h-1}\varepsilon^{l(t+k-i)}.$$

When $t + k - i$ is divisible by the imprimitivity index h, the last sum in the above expression equals h; otherwise elementary trig-

onometrical identities show that this sum vanishes. Thus

$$\mathcal{L}_i(\mathbf{x}, t) = \frac{hc_i}{p'(r)\, r^i} \sum_{\substack{1 \leqslant k \leqslant n \\ k \equiv i-t \pmod h}} r^{k-1} q_k(r) \frac{x_k}{c_k}, \tag{2.55}$$

$$i = 1, 2, \ldots, n,$$

where the summation is taken over all k values that differ from $i - t$ by any number divisibly by h. In a vector form

$$\mathcal{L}(\mathbf{x}, t) = \begin{bmatrix} \varphi_1(\mathbf{x}, t)\, c_1/r \\ \varphi_2(\mathbf{x}, t)\, c_2/r^2 \\ \cdots\cdots \\ \varphi_n(\mathbf{x}, t)\, c_n/r^n \end{bmatrix}, \tag{2.56}$$

where

$$\varphi_i(\mathbf{x}, t) = \frac{h}{p'(r)} \sum_{\substack{1 \leqslant k \leqslant n \\ k = i-t \pmod h}} r^{k-1} q_k(r) \frac{x_k}{c_k}, \quad i = 1, 2, \ldots, n. \tag{2.57}$$

Using the equations (2.56) and (2.57) we can make a number of statements concerning the asymptotic behavior of Leslie model trajectories. When matrix L is primitive, that is $h = 1$, the summation is taken over all indices k from 1 to n and the limit function, thus, does not depend on t:

$$\lim_{t \to \infty} \frac{L^t \mathbf{x}}{r^t} = \lim \mathcal{L}(\mathbf{x}) = \sum_{k=1}^{n} \frac{r^{k-1} q_k(r)\, x_k}{p'(r)\, c_k} \begin{bmatrix} c_1/r \\ c_2/r^2 \\ \cdot \\ \cdot \\ \cdot \\ c_n/r^n \end{bmatrix}. \tag{2.58}$$

The relationship (2.58) is a well-known result of Leslie: for a primitive matrix L the limit distribution is in proportion to the eigenvector corresponding to the largest eigenvalue*, with the proportionality coefficient—denote it by $\varphi(r, \mathbf{x})$—linearly depending on the coordinates of the initial distribution $\mathbf{x}$.

Theorem (about the average cyclic value). *Let h be the imprimitivity index of matrix L. Then*

$$\lim_{t \to \infty} \frac{1}{h} \sum_{j=1}^{h} \frac{L^{t+j}\mathbf{x}}{r^{t+j}} = \varphi(r, \mathbf{x}) \begin{bmatrix} c_1/r \\ c_2/r^2 \\ \cdot \\ \cdot \\ \cdot \\ c_r/r^n \end{bmatrix}, \tag{2.59}$$

* This result was obtained by Leslie for the case where all L eigenvalues are different; notice that to derive (2.58) we did not need this restriction.

where

$$\varphi(r, \mathbf{x}) = \sum_{k=1}^{n} \frac{r^{k-1} q_k(r) x_k}{p'(r) c_k}. \tag{2.60}$$

Proof. From (2.55) the ith coordinate of the limit function for the vector on the left-hand side (2.59), has the form

$$\frac{1}{h} \sum_{j=1}^{h} \frac{h c_i}{p'(r) r^i} \sum_{\substack{i \leqslant k \leqslant n \\ k \equiv i-(t+j) \pmod h}} \frac{r^{k-1} q_k(r) x_k}{c_k}$$

$$= \frac{c_i}{r_i} \sum_{k \in \mathscr{K}(i,\, t)} \frac{r^{k-1} q_k(r) x_k}{p'(r) c_k}, \qquad i = 1, 2, \ldots, n. \tag{2.61}$$

The set of values index k takes on in the double summation of (2.61) is evidently defined as follows

$$\mathscr{K}(i, t) = \{k\colon 1 \leqslant k \leqslant n,$$
$$k - i + (t + j) \equiv 0 \pmod h,\ j = 1, 2, \ldots, h\}.$$

Let us show that $\mathscr{K}(i, t)$ does not depend on i or t but simply coincides with the set $k = 1, 2, \ldots, n$. In fact, let k_0 be a number from this set. Dividing $k_0 - i + t$ by h we get

$$k_0 - i + t = mh + \rho, \qquad 0 \leqslant \rho < h.$$

If the residue $\rho = 0$, the integer $k_0 - i + (t + h)$ can also be divided by h without remainder, i.e. $k_0 \in \mathscr{K}(i, t)$. When $0 < \rho < h$, no remainder is left if we divide $k_0 - i + (t + h - \rho)$ by h, that is again $k_0 \in \mathscr{K}(i, t)$.

Let us show now that each k value can be encountered only once in the double sum (2.61). If there is a pair of indices j_1 and j_2 $(1 \leqslant j_1, j_2 \leqslant h)$ such that

$$k - i + (t + j_1) \equiv 0 \pmod h,$$
$$k - i + (t + j_2) \equiv 0 \pmod h,$$

then

$$j_1 - j_2 \equiv 0 \pmod h,$$

and since both indices j_1 and j_2 themselves cannot exceed h, it follows that

$$j_1 = j_2.$$

Thus

$$\mathscr{K}(i, t) = \{1, 2, \ldots, n\},$$

and the sum (2.61) is nothing but

$$\frac{c_i}{r^i} \sum_{k=1}^{n} \frac{r^{k-1} q_k(r)\, x_k}{p'(r)\, c_k},$$

Q.E.D.

Two following asymptotic properties will go without proofs.

Theorem (about periodicity). *Let h be the imprimitivity index of L. Then the limiting vector function $\mathcal{L}(\mathbf{x}, t)$ is periodic in t with a period*

$$T = \text{L.C.M. } \{v_l\colon (\mathbf{R}_l, \mathbf{x}) \neq 0, \quad l - 1 = (u_l/v_l)\, h\}, \tag{2.62}$$

where l runs through the values $1, 2, \ldots, h$ and u_l/v_l is an irreducible fraction (for $l = 1$, $u_l = 0$, $v_l = 1$).

Thus, T is a divisor for the imprimitivity index h and depends on the initial distribution $\mathbf{x}$.

In particular, $h = 1$ for a primitive matrix L, hence all $v_l = 1$, and their least common multiple $T = 1$. Thus, the limiting function is constant in t; besides, this also follows directly from (2.58).

We now consider the asymptotic behavior of total population number $N(t) = \sum_{i=1}^{n} x_i(t)$ when $\mathbf{x}(t)$ is asymptotically periodic. Clearly

$$N(t) \to \mathcal{N}(\mathbf{x}, t) = \sum_{i=1}^{n} \mathcal{L}_i(\mathbf{x}, t)$$

and if T is the period of $\mathcal{L}(\mathbf{x}, t)$ then

$$N(\mathbf{x}, t + T) = \mathcal{N}(\mathbf{x}, t).$$

Thus the true period of $\mathcal{N}(\mathbf{x}, t)$ at least should be a divisor for T. The conditions that make it equal to T are specified by

Theorem (about the total number period). *Period of the total numbers $\mathcal{N}(\mathbf{x}, t)$ for the asymptotic distribution $\mathcal{L}(\mathbf{x}, t)$ coincides with the period of $\mathcal{L}(\mathbf{x}, t)$ if and only if*

$$\sum_{i=1}^{n} c_i \lambda_l^{n-i} \neq 0, \qquad l = 1, 2, \ldots, h. \tag{2.63}$$

Simple sufficient conditions for (2.63) to hold are provided by

$$\lambda_1 > \max\{s_1, \ldots, s_{n-1}\} \tag{2.64}$$

or

$$\lambda_1 < \min\{s_1, \ldots, s_{n-1}\}. \tag{2.65}$$

The periodicity theorems indicate that the behavior of trajectories radically depends on the chosen time scale: we can avoid cyclicity in model trajectories, for instance, by extending time intervals, so that age groups with non-zero natality become neighboring. On the

other hand, for semelparic organisms the Leslie model can only give asymptotically cyclic trajectories ($b_1 = 0, \ldots, b_{n-1} = 0, b_n > 0$).

As mentioned above, a non-trivial limiting distribution is possible only if the largest eigenvalue $r = 1$, that is when

$$p(1) = 1 - \sum_{i=1}^{n} b_i s_1 s_2 \ldots s_{i-1} = 0,$$

since r is the only positive root of the characteristic polynomial. If this condition is not satisfied, the easiest hypothetical method to redress it is to perform a proportional alteration of all natalities, i.e. to transform

$$\hat{b}_i = kb_i, \qquad k > 0, \tag{2.66}$$

so that

$$\hat{p}(1) = 0 = 1 - \sum_{i=1}^{n} kb_i s_1 s_2 \ldots s_{i-1}. \tag{2.66}$$

As b_i increases, r also increases and, conversely, decreases, as b_i decreases.

From (2.66) the proportionality coefficient will be

$$k = 1 \Big/ \sum_{i=1}^{n} b_i s_1 s_2 \ldots s_{i-1} = \frac{1}{R}. \tag{2.67}$$

The quantity R serves as a generalized parameter of the whole population reproduction rate, i.e. as a kind of stability measure. If $R = 1$, then $r = 1$ and there is no exponential growth or extinction in the population, instead the population approaches a limiting distribution. The cases that $R < 1$ and $R > 1$ correspond to $r < 1$ and $r > 1$, which means that according to (2.53) and (2.56) the population declines to extinction or grows infinitely.

2.6. Classification of stable solutions

In order to clear up the question of the stable trajectories existence in a linear dynamic system

$$\mathbf{x}(t+1) = L\mathbf{x}(t), \qquad t = 0, 1, 2, \ldots, \tag{2.68}$$

given by a Leslie matrix, we shall start, just as in the case of one difference equation (Section 2), by considering the simplest types of solution $\mathbf{x}^*t$—the equilibrium and cycles.

The *equilibrium*, i.e. the solution characterized by

$$\mathbf{x}^* = L\mathbf{x}^*,$$

is nothing but the eigenvector of L, corresponding to the largest eigenvalue $r = 1$. that is positive according to the Perron-Frobenius

theorem. Model linearity provides that for an initial equilibrium perturbation

$$\delta \mathbf{x}(0) = \mathbf{x}(0) - \mathbf{x}^*$$

the deviation $\delta \mathbf{x}(t)$ is governed by the original matrix L:

$$\delta \mathbf{x}(t) = \mathbf{x}(t) - \mathbf{x}^* = L^t \delta \mathbf{x}(0).$$

Expanding $\delta \mathbf{x}(0)$ in Jordan basis vectors, we can easily see that for the deviation $\delta \mathbf{x}(t)$ to be small after a finite number of steps t, the initial displacement should be sufficiently small. Thus, the local stability properties are in the final analysis defined by the asymptotic behavior of $L^t \delta \mathbf{x}(0)$, which in the case of $r = 1$ is described by the limit function $\mathcal{L}[\delta \mathbf{x}(0), t]$. According to (2.55) by choosing a sufficiently small $\delta \mathbf{x}(0)$ we can make the limit function $\mathcal{L}[\delta \mathbf{x}(0), t]$ arbitrarily close to zero, thereby satisfying the formal definition of the Lyapunov local stability. Consequently, if the equilibrium $\mathbf{x}^*$ exists ($r = 1$), it is locally stable. Notice that there can be no asymptotic stability in this case, since for any finite $\delta \mathbf{x}(0)$ the limit function $\mathcal{L}[\delta \mathbf{x}(0), t]$ differs from zero.

All the above can be generalized to the case of any trajectory $\mathbf{x}^*(t)$. In fact, as $t \to \infty$

$$\delta \mathbf{x}(t) = L^t \delta \mathbf{x}(0) \to \begin{cases} \infty, & \text{if } r > 1 \\ 0, & \text{if } r < 1 \\ \mathcal{L}[\delta \mathbf{x}(0), t], & \text{if } r = 1. \end{cases}$$

Thus, when $r > 1$, every solution is unstable.

At $r = 1$ all solutions $\mathbf{x}^*(t)$ exhibit local non-asymptotic stability. Strictly speaking, if matrix L is primitive, $\mathbf{x}^*(t)$ has a limit, as $t \to \infty$, proportional to the steady state with the proportionality coefficient linear with the coordinates of the initial distribution. If the imprimitivity index $h > 1$, every solution which is different from equilibrium tends to a periodic limit function with a period that is a divisor of h and depends on the initial distribution $\mathbf{x}^*(0)$ [see (2.62)]. The deviation from this solution, which is small for sufficiently small $\delta \mathbf{x}(0)$, is also asymptotically periodic with its own period.

For $r < 1$ all the solutions $\mathbf{x}^*(t)$ are globally asymptotically stable, which simply reflects the general picture of the behavior of trajectories, i.e. all trajectories approach a zero distribution.

Can there be purely *cyclic* trajectories or *cycles* in the Leslie model? If vector $\mathbf{x}^{(k)}$ belongs to a cycle of period k, it should satisfy the condition

$$L^k \mathbf{x}^{(k)} = \mathbf{x}^{(k)}. \tag{2.69}$$

Therefore $\mathbf{x}^{(k)}$ is an eigenvector for matrix L^k with an eigenvalue $\mu = 1$. The same holds for all the other vectors comprising the

k-cycle. Since eigenvalues L^k equal λ^k, where λ are the eigenvalues of L, a unitary eigenvalue for L^k can only occur when there is a kth root of 1 in the spectrum of L. Clearly, in this case $r \geqslant 1$. Since $r > 1$ corresponds to trajectory instability, we shall restrict ourselves to the case of $r = 1$. Then all the roots with absolute values of 1 fit the equation $\lambda^h - 1 = 0$; accordingly, $\lambda^h = 1$ indicates that the numbers k and h have common divisors. In what follows we will show that actually the cycle period k is a divisor for h.

If matrix L is primitive, its every natural degree L is indecomposable and primitive, and according to the Perron-Frobenius theorem, has a maximal root $r^t = 1$ of unit multiplicity. Thus the vectors $\mathbf{x}^k(0)$, $\mathbf{x}^k(1)$, ..., $\mathbf{x}^k(k-1)$, which comprise the k-cycle, belong to one and the same positive characteristic direction, that is

$$\mathbf{x}^{(k)}(j) = \theta_j \mathbf{x}^{(k)}(0), \qquad \theta_j > 0, \qquad j = 1, 2, \ldots, k-1.$$

The sense of the cycle suggests

$$L\mathbf{x}^{(k)}(0) = \mathbf{x}^{(k)}(1) = \theta_1 \mathbf{x}^{(k)}(0),$$

therefore $\mathbf{x}^{(k)}(0)$ is an eigenvector of L with the eigenvalue $\theta_1 > 0$. But since the only positive eigenvalue of L is $r = 1$, it follows that $\theta_1 = 1$ and

$$x^{(k)}(1) = x^{(k)}(0).$$

Reasoning along the same line we obtain the chain of equalities

$$\mathbf{x}^{(k)}(0) = \mathbf{x}^{(k)}(1) = \ldots = \mathbf{x}^{(k)}(k-1),$$

i.e. our k-cycle in fact is simply an equilibrium. For primitive Leslie matrices with $r = 1$, cycles are impossible.

The same result follows from other considerations. Since every initial distribution as $t \to \infty$ tends to the limiting vector function $\mathcal{L}(\mathbf{x}, t)$, which is constant in t in the primitive case, cycles possibly cannot occur.

When the imprimitivity index $h > 1$, the periodic limit function $\mathcal{L}(\mathbf{x}, t)$ itself falls into an exact cycle. In fact, from (2.54) and allowing $r = 1$ we get

$$L\mathcal{L}(\mathbf{x}, t) = \sum_{l=1}^{h} \varepsilon^{(l-1)t} (\mathbf{R}_l, \mathbf{x}) L\mathbf{C}_l$$

$$= \sum_{l=1}^{h} \varepsilon^{(l-1)t} (\mathbf{R}_l, \mathbf{x}) \varepsilon^{l-1} \mathbf{C}_l = \mathcal{L}(\mathbf{x}, t+1) \qquad (2.70)$$

The period of this cycle is determined evidently by the period T of the function $\mathcal{L}(\mathbf{x}, t)$ which, by the theorem of the preceding section, is a divisor of h.

If system (2.68) had a true cycle of period k different from the divisors of h, the trajectory initiating from one of the vectors $\mathbf{y}^{(k)}$

of this cycle, would be approaching $\mathcal{L}(\mathbf{y}^{(h)}, t)$. Then the period of $\mathcal{L}(\mathbf{y}^{(h)}, t)$ would be a divisor of h, which leads us to a contradiction.

Thus for a Leslie matrix cycles are only possible of such a period k which is a divisor for the imprimitivity index h. All these cycles belong to the subspace of the matrix L eigenvectors that corresponds to the largest eigenvalue 1 of multiplicity h. Denote this subspace by $\Lambda^{(h)}$. Since the geometric multiplicity of an eigenvector is less than or equal to its algebraic multiplicity, we have

$$\dim \Lambda^{(h)} \leqslant h. \tag{2.71}$$

On the other hand, from the relationship (2.70), and the theorem concerning periodicity, it follows that for every initial vector $\mathbf{x}$

$$L^{(h)}\mathcal{L}(\mathbf{x}, t) = \mathcal{L}(\mathbf{x}, t+h) = \mathcal{L}(\mathbf{x}, t),$$

that is the space of all possible vectors $\mathcal{L}(\mathbf{x}, t)$ belongs to $\Lambda^{(h)}$:

$$\{\mathcal{L}(\mathbf{x}, t)\} \subset \Lambda^{(h)}. \tag{2.72}$$

But, by (2.54), vectors $\{\mathcal{L}(\mathbf{x}, t)\}$ represent linear combinations of eigenvectors $\mathbf{C}_1, \ldots, \mathbf{C}_h$ of matrix L, which correspond to different eigenvalues $1, \exp(i2\pi/h), \ldots, \exp(i2\pi(h-1)/h)$ and therefore are linearly independent. Thus

$$\dim \{\mathcal{L}(\mathbf{x}, t)\} = h, \tag{2.73}$$

which in combination with (2.71) and (2.72) means that both spaces coincide

$$\{\mathcal{L}(\mathbf{x}, t)\} = \Lambda^{(h)}. \tag{2.74}$$

Thus the true cycles in system (2.68) with an imprimitive matrix L are the trajectories made by vectors of the form $\mathcal{L}(\mathbf{x}, t)$ with a period that divides h and depends on $\mathbf{x}$ according to (2.62). Notice that there are cycles of period 1 in $\{\mathcal{L}(\mathbf{x}, t)\}$, i.e. equilibria. These are simply vectors belonging to the characteristic direction for the eigenvalue $r = 1$, i.e. proportional to $\mathbf{C}_1$. In fact, when

$$\mathbf{x} = a\mathbf{C}_1, \qquad a > 0,$$

we have by (2.52)

$$\mathcal{L}(a\mathbf{C}_1, t) = \sum_{l=1}^{h} \varepsilon^{(l-1)t}(\mathbf{R}_l, a\mathbf{C}_1)\,\mathbf{C}_l = a\mathbf{C}_1.$$

In particular, when $h = n$, we have the equality

$$L^{(h)} = I, \tag{2.75}$$

where I is the identity matrix. It means that every vector $\mathbf{x}$ is transformed into itself after n steps, in other words, $\mathbf{x}$ belongs to a cycle with a period equal to n or a divisor n. Matrices L with the property (2.75) correspond to semelparity, when parents die after one act

of reproduction. An example is given by matrix

$$L = \begin{Vmatrix} 0 & 0 & 6 \\ 1/2 & 0 & 0 \\ 0 & 1/3 & 0 \end{Vmatrix}, \tag{2.76}$$

treated by G. Bernadelli as a model of "population waves".

Concerning the *chaotic* behavior, that is such trajectories $\mathbf{x}^*(t)$ which are neither constant nor periodic and do not tend to any constant distribution or a cycle, we can be sure that such a behavior is impossible for system (2.68) with $r = 1$, since for every $\mathbf{x}(t) = L^t\mathbf{x}$ there exists a limit function $\mathcal{L}(\mathbf{x}, t)$ that is either constant or periodic. When $r < 1$ all trajectories tend to zero. When $r > 1$, $L^t\mathbf{x}$ has no limit, however there is a limit for $L^t\mathbf{x}/r^t$, i.e.

$$\mathbf{x}(t) \to r^t \mathcal{L}(\mathbf{x}, t)$$

and "chaos" in this case has quite an ordered structure: trajectories approach a limiting vector function which grows r-fold with every step in time.

Example. Consider a hypothetical population, comprising $n = 6$ age groups, chosen such that only the third and sixth groups are fertile. Let

$$b_3 = b_6 = 4,$$

and the survival coefficients s_i be such that

$$L = \begin{Vmatrix} & 0 & 4 & 0 & 0 & 4 \\ 1/3 & & & & & \\ & 1/2 & & 0 & & \\ & & 1/2 & & & \\ 0 & & & 1 & & \\ & & & & 1 & \end{Vmatrix}$$

And we easily find that the characteristic polynomial

$$p(\lambda) = \lambda^6 - \frac{2}{3}\lambda^3 - \frac{1}{3},$$

the largest eigenvalue

$$r = \lambda_1 = 1,$$

and the imprimitivity index

$$h = \text{GCD}\ (3,6) = 3,$$

hence the system can have only equilibria and 3-cycles. A short calculation yields

$$\lambda_2 = \varepsilon = e^{i2\pi/3}, \qquad \lambda_3 = \varepsilon^2,$$

$$\varepsilon + \varepsilon^2 = -1,$$

$$\lambda_4 = e^{i\pi/3}\sqrt[3]{3}, \qquad \lambda_5 = e^{i\pi}\sqrt[3]{3}, \qquad \lambda_6 = e^{i5\pi/3}\sqrt[3]{3}.$$

We find from (2.51) that the eigenvector-rows are:

$$\mathbf{R}_1 = \frac{1}{2}[1,\ 3,\ 6,\ 4,\ 4,\ 4],$$

$$\mathbf{R}_2 = \frac{1}{2}[1,\ 3\varepsilon,\ 6\varepsilon^2,\ 4,\ 4\varepsilon,\ 4\varepsilon^2],$$

$$\mathbf{R}_3 = \frac{1}{2}[1,\ 3\varepsilon^2,\ 6\varepsilon,\ 4,\ 4\varepsilon^2,\ 4\varepsilon].$$

And for the eigenvector-columns we get:

$$\mathbf{C}_1 = \frac{1}{2}\begin{bmatrix} 1 \\ 1/3 \\ 1/6 \\ 1/12 \\ 1/12 \\ 1/12 \end{bmatrix}, \qquad \mathbf{C}_2 = \frac{1}{2}\begin{bmatrix} 1 \\ \varepsilon^3/3 \\ \varepsilon/6 \\ 1/12 \\ \varepsilon^2/12 \\ \varepsilon/12 \end{bmatrix}, \qquad \mathbf{C}_3 = \frac{1}{2}\begin{bmatrix} 1 \\ \varepsilon/3 \\ \varepsilon^2/6 \\ 1/12 \\ \varepsilon/12 \\ \varepsilon^2/12 \end{bmatrix}.$$

Every distribution of numbers which is proportional to the vector $\mathbf{C}_1$, remains constant at any step. All the other distributions $\mathbf{x}$ approach with time a 3-cycle made up of the vectors $\mathcal{L}(\mathbf{x}, 0)$, $\mathcal{L}(\mathbf{x}, 1)$ and $\mathcal{L}(\mathbf{x}, 2)$. Let the population be initially equally distributed into groups, for instance, in the following way:

$$\mathbf{x} = [16,\ 16,\ 16,\ 16,\ 16,\ 16]^T.$$

Then

$$\mathcal{L}(\mathbf{x}, 0) = \sum_{l=1}^{3} (\mathbf{R}_l, \mathbf{x})\,\mathbf{C}_l =$$

$$= 88\begin{bmatrix} 1 \\ 1/3 \\ 1/6 \\ 1/12 \\ 1/12 \\ 1/12 \end{bmatrix} + 4(5 + 7\varepsilon + 10\varepsilon^2)\begin{bmatrix} 1 \\ \varepsilon^2/3 \\ \varepsilon/6 \\ 1/12 \\ \varepsilon^2/12 \\ \varepsilon/12 \end{bmatrix} +$$

$$+ 4(5 + 10\varepsilon + 7\varepsilon^2)\begin{bmatrix} 1 \\ \varepsilon/3 \\ \varepsilon^2/6 \\ 1/12 \\ \varepsilon/12 \\ \varepsilon^2/12 \end{bmatrix} = \begin{bmatrix} 60 \\ 28 \\ 20 \\ 5 \\ 7 \\ 10 \end{bmatrix},$$

$$\mathscr{L}(\mathrm{x}, 1) = L\mathscr{L}(\mathrm{x}, 0) = \begin{bmatrix} 120 \\ 20 \\ 14 \\ 10 \\ 5 \\ 7 \end{bmatrix}$$

$$\mathscr{L}(\mathrm{x}, 2) = L\mathscr{L}(\mathrm{x}, 1) = \begin{bmatrix} 84 \\ 40 \\ 10 \\ 7 \\ 10 \\ 5 \end{bmatrix}.$$

Thus a trajectory, initiating from $\mathrm{x} = [16, 16, 16, 16, 16, 16]^T$, tends to a 3-cycle built on vectors

$[60, 28, 20, 5, 7, 10]^T$,

$[120, 20, 14, 10, 5, 7]^T$,

$[84, 40, 10, 7, 10, 5]^T$.

The rate of convergence is given by $(1/\sqrt[3]{3})^t \approx 0.693^t$; it means that after 6 generations the difference between the initial and the limiting distribution decreases approximately 10-fold, and after 12 generations—approximately 100-fold, and so on.

The conditions given by (2.63) are satisfied and the total number $N(t)$ also approach a 3-cycle comprising the values 130, 176, 156.

2.7. Leslie model applications

When using the Leslie model for natural population analysis a number of difficulties arise connected with the limitations on the model. Thus, for example, for reasons of specific restrictions on experiments and observations it is often impossible to consider specimens of only the last fertile age in the last, nth, age group. In this case all the elder specimens are also referred to the nth group, but an element p_n $(0 < p_n < 1)$ is added to the Leslie matrix. It stands for the fraction of the nth group specimens, that survive after one time

interval. Matrix L is thus rearranged to give

$$L+\Delta(p_n)=\begin{Vmatrix} b_1 & b_2 & \dots & b_{n-1} & b_n \\ s_1 & 0 & & & 0 \\ & & \ddots & & \\ & s_2 & & 0 & \\ & & \ddots & & \\ 0 & & & & \\ & & & s_{n-1} & p_n \end{Vmatrix} \tag{2.77}$$

and

$$x_n(t+1)=s_{n-1}x_{n-1}(t)+p_nx_n(t).$$

Such a construction results in a non-zero part of the population living indefinitely; the systematic relative error appearing as a consequence does not exceed the sum

$$p_n^{M+1}+p_n^{M+2}+\dots=p_n^{M+1}/(1-p_n),$$

where M is the maximal possible age of individual organisms.

Another difficulty arises because it is not always possible to choose a time scale, such that successive points in time $t=1, 2, \dots$ correspond to the transitions of organisms from one age group to the next one. One can use the following method in this case: along with the quantities s_i the variables p_i are introduced $(0<p_i<1)$, which stand for the fraction of the ith group organisms, that by the next time t did not mature enough to transfer to the next age class. Then matrix L takes the form

$$L+\Delta(p_1, p_2, \dots, p_n)=\begin{Vmatrix} b_1+p_1 & b_2 & \dots & b_{n-1} & b_n \\ s_1 & p_2 & & & 0 \\ & & \ddots & & \\ & s_2 & & p_{n-1} & \\ & & \ddots & & \\ 0 & & & & \\ & & & s_{n-1} & p_n \end{Vmatrix}. \tag{2.78}$$

The modified matrices (2.77) and (2.78) retain the basic property of the classical Leslie matrix—the non-negativity of its elements. Thus the Perron-Frobenius theorem is still valid and in the primitive case there exists a limit

$$\lim_{t\to\infty}\frac{(L+\Delta)^t\mathbf{x}}{r^t}=\varphi(r, \mathbf{x})\,\mathbf{C}_1$$

where C_1 is the eigenvector belonging to the largest eigenvalue $r(L + \Delta)$ of the modified matrix. Moreover, since all the matrix entries are non-negative, the relation

$$L \leqslant L + \Delta$$

is satisfied, whence it follows* that

$$r(L) < r(L + \Delta),$$

i.e. the modification makes the model less stable in relation to the initial matrix L. If we want the modified matrix to keep stable the trajectories of the original matrix in the case that $r(L) = 1$, we will have to change the matrix L elements so that $r(L + \Delta) = 1$.

Evaluating the behavior of the Leslie model trajectories as a whole, it should be noted that the use of this model for simulating natural populations dynamics has severe constraints associated with the cycles period. Population cycles typical for many populations can result in the model only when their period does not exceed the life-span of one specimen; the matrix in this case should be constructed in such a way that its imprimitivity index would either be divisible by, or equal to, the cycle period. Besides, the absence of chaotic behavior indicates, that in spite of a more complex (due to the introduction of age groups) population structure, the linearity of interaction mechanisms significantly narrows the qualitative diversity of trajectories compared with the homogeneous population dynamics with self-limiting in numbers (Section 2.4).

One of the attempts to reconcile the analytical simplicity of the linear Leslie model with complicated dynamics of natural populations resulted in the so-called model of a "matrix jump". Cyclic, or almost cyclic, population dynamics is modeled using two Leslie matrices, differing from one another by the set of survival coefficients s_i in such a way that one of them (L_1) has the largest eigenvalue $r_1 > 1$, while the other one (L_2) has $r_2 < 1$ ($r_1 r_2 = 1$). When the total number $N(t)$ of the population modeled is less than some average (fixed) value $\bar{N}$, say $\bar{N} = 1000$, the population is governed by matrix L_1 that provides an increase in number. As soon as $N(t)$ overgrows $\bar{N}$, the population operation is switched to matrix L_2 that produces a decrease in number. We see that the concept of cyclicity is built into the model structure itself; however, as yet there are no strict analytical results concerning cycles in the "matrix jump" model. Model trajectories can easily be obtained with a computer. They show a wide variety of "quasicycles", i.e. trajectories formed by numbers in groups rounded off to integers. Such "quasicycles" successfully reflect the natural population dynamics, e.g. in mammals, with cycle periods of several years.

* Gantmacher, F. R., *The Theory of Matrices*, Chelsea, New York, 1960.

On the theoretical side, however, it would be more adequate to recognize that in real life the fertilities and mortalities in different age groups depend upon the densities of either these groups themselves or the population as a whole. Leslie model generalization of this kind are considered in the following section.

2.8. Constraints on Leslie model

The classical Leslie model presupposes the fertility and mortality values to be constant with no relation to population density. Accounting for factors, that depend on the numbers of age groups, we get the general model of population dynamics in the form

$$\mathbf{x}(t+1) = L_{x(t)}\,\mathbf{x}(t), \tag{2.79}$$

where the elements of matrix L_x are functions of the number vector $\mathbf{x}$.

The analytical methods for a first order dynamic system (2.3) can easily be generalized to system (2.79) that gives the dynamics of n-dimensional vectors. The equilibrium $\mathbf{x}^*$ is found as the solution to equation

$$\mathbf{x}^* = L_{x^*}\mathbf{x}^*, \qquad \mathbf{x}^* > 0, \tag{2.80}$$

which indicates that there exists such a set of numbers $\mathbf{x}^*$, and that matrix L_{x^*} has a unitary eigenvalue; then $\mathbf{x}^*$ is the eigenvector belonging to this value. Equation (2.80) is a non-linear eigenvalue problem. For some classes of these problems, theorems generalizing the results of the Perron-Frobenius theorem are proved, but how to find the eigenvectors entirely depends on the functions chosen for L_x. Notice that the "matrix jump" model described above represents a special case of system (2.79) with a step function of the form

$$L_x = \begin{cases} L_1, & \text{if } \sum\limits_{i=1}^{n} x_i \leqslant \bar{N}, \\ L_2, & \text{if } \sum\limits_{i=1}^{n} x_i > \bar{N}. \end{cases}$$

The discontinuity of the functions prohibits linearization, a traditional method of stability analysis. When the functions comprising L_x are sufficiently smooth, the linearization of (2.79) about $\mathbf{x}^*$ to the terms of second order gives

$$\mathbf{x}(t+1) = L_{x^*}\mathbf{x}^* + \left(L_{x^*} + \sum_{i=1}^{n} \left(\frac{\partial L}{\partial x_i}\right)_* X_i^*\right)(\mathbf{x}(t) - \mathbf{x}^*), \tag{2.81}$$

where $(\partial L/\partial x_i)_*$ is a matrix with elements obtained through differentiation of L entries with respect to x_i at the point $\mathbf{x}^*$, and matrix X_i^* has a single non-zero ith column, equal to vector $\mathbf{x}^*$.

Denoting the displacement from equilibrium by $\delta \mathbf{x} = \mathbf{x} - \mathbf{x}^*$, we get

$$\delta \mathbf{x}\,(t+1) = L_\delta \delta \mathbf{x}\,(t),$$

where

$$L_\delta = \sum_{i=1}^{n} \left(\frac{\partial L}{\partial x_i}\right)_* X_i^* + L_{x*}. \tag{2.82}$$

Notice that matrix L_δ is already independent of t, so that

$$\delta \mathbf{x}\,(t) = L_\delta^t \delta \mathbf{x}\,(0),$$

and we can judge about the stability of equilibrium $\mathbf{x}^*$ by the spectrum of L_δ. If the largest (by absolute value) eigenvalue ξ of matrix L_δ—let us call it *dominant*—exceeds 1 in absolute value, the deviations $\delta \mathbf{x}\,(t)$ from equilibrium increase with time, that is the equilibrium is unstable. If $|\xi| < 1$ the deviations decline with time and $\mathbf{x}^*$ is stable (asymptotically). When $|\xi| = 1$, we need to examine higher order terms in the expansion (2.81). In all cases, except when $\xi > 0$, oscillatory behavior is to be expected around equilibrium.

In practice the more specific case of system (2.79) operates well enough. Supposing that all the natality and survival coefficients depend only on the total of all age groups numbers $N(\mathbf{X})$, we get

$$\mathbf{x}\,(t+1) = L_{N[x(t)]}\mathbf{x}\,(t). \tag{2.83}$$

Now the problem (2.80) is reduced to looking for a number N^*, such that matrix L_{N*} has an eigenvalue $\lambda = 1$, that is N^* are the positive solutions to the equation

$$\det\,(L_{N*} - I) = 0$$

For each $N^* > 0$ obtained the equilibrium $\mathbf{x}^* > 0$ is determined as an eigenvector of the numerical matrix $L_{N*} \geqslant 0$, corresponding to the eigenvalue $\lambda = 1$ (which exists by the Perron-Frobenius theorem), and normalized so that for the coordinate sum we have

$$\sum_{i=1}^{n} x_i^* = N^*.$$

The linearization matrix (2.82) is reduced in this case to

$$L_\delta = L_{N*} + \left(\frac{\partial L}{\partial N}\right)_* X^*, \tag{2.84}$$

where matrix X^* contains n identical columns $\mathbf{x}^*$.

A simplest example of this kind was suggested by P. Leslie himself in his second paper dealing with the use of matrices in population

dynamics. He assumed that all the elements of a constant matrix L with the dominant value $\lambda_1 > 0$ vary with N so that the dominant value for matrix L_N equals $\lambda_1/q(N)$, where $q(N)$ is a linear function of the total number N. Actually it means that all the elements of L are multiplied by one and the same number $1/q(N)$, that is all the non-zero natalities and survivals have a similar dependence on N, and (2.83) takes the form

$$\mathbf{x}(t+1) = L\mathbf{x}(t)/q(N), \tag{2.85}$$

where L is a Leslie matrix with constant coefficients and dominant value λ_1.

The equilibrium $\mathbf{x}^*$ here exists if

$$\lambda_1/q(N^*) = 1$$

and is represented by the dominant eigenvector of matrix L. Since the sum of coordinates $\mathbf{x}^*$ should satisfy the above relation, the equilibrium $\mathbf{x}^*$ is now determined uniquely and not up to a constant as in the classical Leslie model. When the population N is so small that it has neither a stimulating nor a stabilizing effect, it is controlled by the matrix L, i.e.

$$q(0) = 1.$$

For these reasons for a linear function $q(N)$ we have

$$q(N) = 1 + \frac{\lambda_1 - 1}{K} N, \tag{2.86}$$

where $K = N^*$ is the population number in the state of equilibrium $\mathbf{x}^*$.

If $\mathbf{x}(t)$ is a steady-state age distribution at time t (proportional to $\mathbf{x}^*$), then

$$\mathbf{x}(t+1) = \frac{L\mathbf{x}(t)}{q[N(t)]} = \frac{\lambda_1 \mathbf{x}(t)}{q[N(t)]}$$

and summing the vector $\mathbf{x}(t+1)$ coordinates, by (2.86), gives

$$N(t+1) = \frac{\lambda_1 N(t)}{1 + (\lambda_1 - 1) N(t)/K}.$$

We easily find that the solution to this difference equation is

$$N(t) = \frac{K}{1 + Ce^{-rt}}, \tag{2.87}$$

where the constant C is

$$C = \frac{K - N(0)}{N(0)},$$

and $r = \ln \lambda_1$. Equation (2.87) corresponds to the solution of a logistic equation. Thus, if the population (2.85) has an age distribution

stationary for matrix L, the total number varies according to the logistic equation for fixed age distribution.

To the question of how the total number varies in case of a non-stationary initial distribution, Leslie's theory gives no definite answer. Some statements about the number variations in this case enable the stability analysis of the equilibrium $\mathbf{x}^*$ to be made. Linearizing (2.85) in the neighbourhood of $\mathbf{x}^*$ we get the matrix

$$L_\delta = \frac{L}{q(N^*)} + [q^{-1}(N)]'_* LX^* = \frac{1}{\lambda_1}\left(L + \frac{1-\lambda_1}{K} X^*\right). \tag{2.88}$$

We now find the dominant value for matrix L. Because

$$L_\delta \mathbf{x}^* = \frac{1}{\lambda_1}\left(L\mathbf{x}^* + \frac{1-\lambda_1}{K} X^*\mathbf{x}^*\right)$$
$$= \frac{1}{\lambda_1}\left(\lambda_1\mathbf{x}^* + \frac{1-\lambda_1}{K} N^*\mathbf{x}^*\right) = \frac{1}{\lambda_1}\mathbf{x}^*,$$

the vector $\mathbf{x}^*$, being an eigenvector for L, is also an eigenvector for L_δ, the corresponding eigenvalue being $1/\lambda_1 > 0$. When $\lambda_1 < 1$, we can show that $\xi = 1/\lambda_1$ is the dominant value. In fact, in this case it follows from (2.88) that matrix L_δ is positive, and consequently, by the Perron theorem, it has the dominant value $\mu > 0$ with the corresponding eigenvector $\mathbf{y} > 0$. Supposing that $\mu \neq \xi$ vectors $\mathbf{x}^*$ and $\mathbf{y}$ are linearly independent, and it turns out that an indecomposable positive matrix L_δ has two linearly independent positive eigenvectors, which is impossible*. In consequence, at $\lambda_1 < 1$ the number $\xi = 1/\lambda_1 > 1$ is dominant for matrix L_δ, and hence the equilibrium $\mathbf{x}^*$ is (monotonically) unstable.

In the case that $\lambda_1 > 1$ the analysis becomes much more complicated, since L_δ is not non-negative any more and the Perron-Frobenius theorem cannot be used. The consideration of numerous examples suggests the following hypothesis: if the original matrix L is primitive, $\xi = 1/\lambda_1 < 1$ is a dominant number for L_δ and equilibrium $\mathbf{x}^*$ is stable and is approached in asymptotic oscillations, consequently, the behavior of the total number $N(t)$ is asymptotically close to the logistic one given by (2.87); when L is imprimitive, L_δ has dominant numbers ξ, such that $|\xi| = 1 > 1/\lambda_1$ and the analysis of stability of $\mathbf{x}^*$ requires an account of higher than first-order terms in the expansion (2.81). Thus, introducing a dependence on population number even in the fairly artificial construction, such as (2.85)-(2.86), we fail to get a simple answer to the stability problem.

The next thing we can do to make the model (2.85) more realistic, is to assume that, the dependence on N of natalities and survivals is different, but similar throughout the age groups. In some cases this already gives an adequate description of the natural population

* Gantmacher, F. R., *The Theory of Matrices*, Chelsea, New York, 1960.

dynamics. An example of system (2.83) used to model laboratory population dynamics for the collembolan *Folsomia candida*, subdivided into 4 weekly age groups, is given by

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ x_4(t+1) \end{bmatrix} = \begin{Vmatrix} 0 & 0 & F(N) & F(N) \\ S(N) & 0 & 0 & 0 \\ 0 & S(N) & 0 & 0 \\ 0 & 0 & S(N) & 0 \end{Vmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ x_4(t) \end{bmatrix}. \tag{2.89}$$

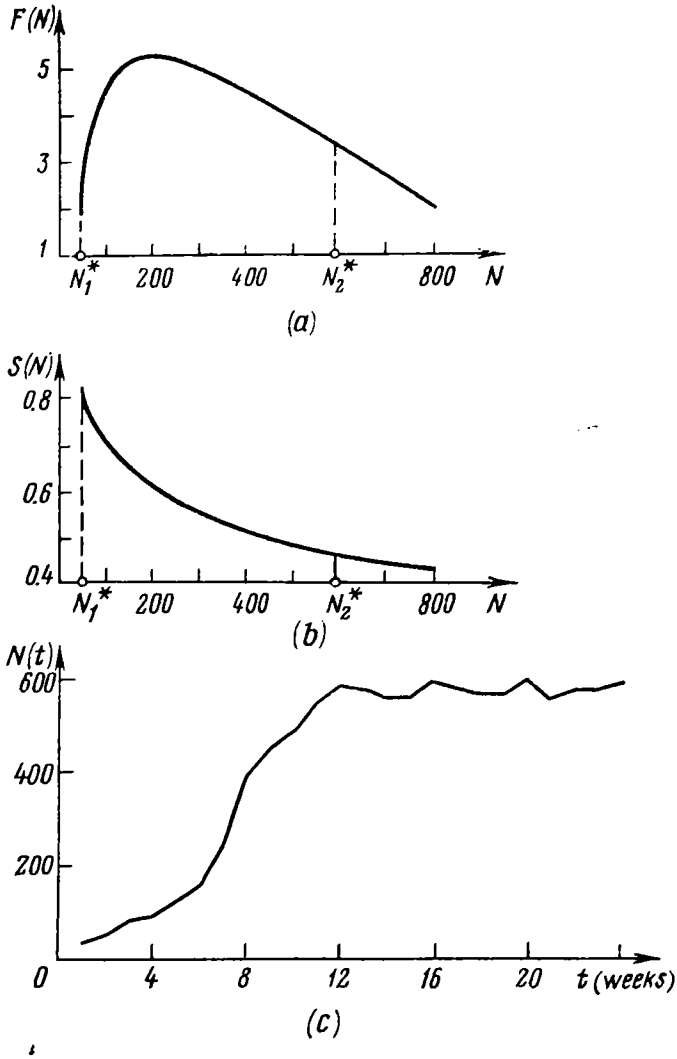

Fig. 10. Fertility and survival as functions of the total population, and total population dynamics in a laboratory culture of collembolan *Folsomia candida*: (*a*) $F(N) = 18.53 \ln N - 1.74 (\ln N)^2 - 44.04$; (*b*) $S(N) = 1.35 - 0.14 \ln N$; (*c*) sigma-like type of population growth.

Relationships $F(N)$ and $S(N)$ observed in experiments had the form as shown in Fig. 10*a*, *b*. These curves may be reproduced, for

instance, by the functional forms

$$F(N) = a \ln N + b (\ln N)^2 + c;$$

$$S(N) = d - e \ln N,$$

their choice being determined by a purely technical convenience of representing N on the logarithmic scale. Numerical values of parameters a, b, c, d and e were found from the regression of experimental data by the least squares method, and afterwards the evaluation of equilibrium values N^* could be reduced to the solution of the transcendental equation for N^*:

$$\det \begin{Vmatrix} -1 & 0 & F(N^*) & F(N^*) \\ S(N^*) & -1 & 0 & 0 \\ 0 & S(N^*) & -1 & 0 \\ 0 & 0 & S(N^*) & -1 \end{Vmatrix} = 0.$$

For fixed parameters values (cf. Fig. 10*a*, *b*) this equation has two positive roots $N_1^* \approx 41.13$ and $N_2^* \approx 596.45$ with the corresponding equilibrium distributions $\mathbf{x}_1^*$ and $\mathbf{x}_2^*$. Calculating the spectrum of matrix L_δ (2.84) for the system (2.89) at the points $\mathbf{x}_1^*$ and $\mathbf{x}_2^*$, we see that in the first caso the dominant value $\xi(\mathbf{x}_1^*) > 1$, i.e. the equilibrium $\mathbf{x}_1^*$ is unstable, and in the second case the dominant values are a pair of complex conjugate numbers $\xi_{1,2}$, $|\xi_t| < 1$, so that at $\mathbf{x}_2^*$ the system reaches equilibrium with asymptotically stable oscillations. These conclusions are verified by the experimental curve of behavior of N (Fig. 10*c*), which grows in a sigma-like manner up to a value of about N_2^*.

Thus, even the simplest form (2.89) of taking into account the limiting factors, furnishes an adequate simulation of population dynamics with a Leslie model. Apparently this explains the widespread use of the model modifications not only to represent the age structure dynamics, but also to tackle problems of optimal population management, of optimal life-cycle strategies, and so on.

It is to be noted, however, that in Leslie model generalizations the search for steady states (let alone cycles) and their stability analysis become much more complex, and since the very first step calls for the solution of a transcendental equation, it is impossible to suggest any general regular method of stability analysis that would give definite conclusions, as to the system dynamics only from the form of matrix L, as it was the case, say, in the classical Leslie model.

It follows from example (2.89), that quite realistic are situations in which we are interested in the stability not of the age distribution $\mathbf{x}^*$ but of the total population $N(t)$. Clearly the latter is a cause of the former. In formal terms it follows from the fact that convergence

in Euclidean norm is equivalent to the convergence in norm

$$\|\mathbf{x}\|_{\Sigma} = \sum_{i=1}^{n} |x_i|.$$

And this in turn means that (as $t \to \infty$) there is a convergence to zero of the expression

$$\|\mathbf{x}(t) - \mathbf{x}^*\|_{\Sigma} = \sum_i |x_i(t) - x_i^*| \geqslant \left|\sum_i (x_i(t) - x_i^*)\right| = |N(t) - N|.$$

From this estimate it is also apparent that the convergence of $N(t)$, generally speaking, does not provide the convergence of distribution $\mathbf{x}(t)$, i.e. the total population stability is a weaker property, than the stability of age distribution. In a classical Leslie model, $N(t)$ stability can be realized along with $\mathbf{x}(t)$ instability, perhaps, only for specially chosen coefficients. But in more realistic models—with the introduction of limiting factors—the study of these situations is of certain interest from mathematical, as well as ecological, point of view.

2.9. Notes and bibliography

To 2.1. Details of the delayed effects in population dynamics and methods of their incorporation into models can be found in the books:

Maynard Smith J., *Models in ecology*, Cambridge University Press, Cambridge, 1974;

May R. M., *Stability and complexity in model ecosystems*, Princeton Univ. Press, Princeton, 1973.

To 2.2. A good survey of applications of simple difference equations to population dynamics is given in the paper:

May R. M., Oster G. F., "Bifurcations and dynamical complexity in simple ecological models," *Amer. Natur.*, **110**, 974, pp. 573-599, 1976.

Examples of applications of equation (2.5) can be found in the book:

Maynard Smith J., *Mathematical ideas in biology*, Cambridge Univ. Press, Cambridge, 1968.

A wider spectrum of examples of trajectories of equation (2.6) is given in the paper:

May R. M., "Biological populations obeying difference equations: stable points, stable cycles, and chaos," *J. Theor. Biol.*, **51**, 2, pp. 511-524, 1975.

Numerous data on applications of equation (2.7) for describing insect population dynamics under laboratory and natural conditions are summarized in the work:

Hassel M. P., Lawton J. H., May R. M., "Patterns of dynamical behavior in single-species populations," *J. Anim. Ecol.*, **45**, 2, pp. 471-486, 1976.

Applications of the equation $N_{t+1} = N_t^{(1-b)/\alpha}$ to an extensive evidence concerning birds, mammals, insects populations are discussed in the article:

Stubbs Mary, "Density dependence in the life-cycles animals and its importance in *K*- and *r*-strategies," *J. Anim. Ecol.*, **46**, 2, pp. 677-688, 1977,

where the connection between the equation parameters and the concepts of K- and r-strategies of selection is discussed as well.

To 2.3. The reader interested in mathematical details is referred to the paper:

Jacobson M. V., "*On the dynamic systems properties, generated by the mapping* $x \to Axe^{-\beta x}$," In: "*Modeling of biological communities*," Vladivostok, Far-Eastern scientific center of AS USSR, pp. 141-162 (in Russian), 1975,

where the dynamics of (2.6) is studied in detail from the viewpoint of the modern theory of dynamic systems.

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The general theorem about the existence of chaotic behavior in equation (2.3) is proved in the paper:

Li T.-Y., Yorke J. A., "Period three implies chaos," *Amer. Math. Monthly*, 82, 10, pp. 982-985, 1975.

Effects of delays for more than one generation are examined in the work:

Levin S. A., May R. M., "A note on difference-delay equations," *Theor. Pop. Biol.*, 9, 2, pp. 178-187, 1976,

where the equation $N_{t+1} = N_t F(N_{t-T})$ is studied.

To 2.4. The Leslie model owes its name to two fundamental papers by P. H. Leslie:

Leslie P. H., "On the use of matrices in certain population mathematics," *Biometrika*, 33, 3, pp. 183-212, 1945;

Leslie P. H., "Some further notes on the use of matrices in population mathematics," *Biometrika*, 35, 3-4, pp. 213-245, 1948,

though matrices have been used in earlier works for age-structure account:

Bernadelli H., "Population waves," *J. Burma Res. Soc.*, 31, 1, pp. 1-18, 1941,

whence the example (2.76) is taken from, and

Lewis E. G., "On the generation and growth of a population," *Sankhya*, 6, pp. 93-96, 1942.

The equations of the matrix model separately for the male and female populations are thoroughly derived in:

Zuber Ye. I., Kolker Yu. I., Poluektov R. A., "*Population numbers and age-structure control*," Nauka, Moscow, pp. 129-138. (Problems of Cybernetics; Vol. 25)* (in Russian).

To 2.5 and 2.6. The relationship between Leslie matrix primitivity and stability of the steady-state distribution was brought out in:

Lopez A., "Problems in stable population theory," Office of population research, Princeton, 1961;

Sykes Z. M., "On discrete stable population theory," *Biometrics*, 25, 2, pp. 285-293, 1969.

The proof of theorems about the primitivity conditions and the imprimitivity index for a Leslie matrix using graph representations of matrices is provided in:

Demetrius L., "Primitivity conditions for growth matrices," *Math. Biosci.*, 12, 1/2, pp. 53-58, 1971.

Leslie matrix analysis from the viewpoint of ergodicity theory is presented in:

Parlett B., "Ergodic properties of population. I. The one-sex model," *Theor. Pop. Biol.*, 1, 2, pp. 191-207, 1970;

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* The Leslie matrix primitivity conditions are slightly in error.

Demetrius L., "Isomorphism of population models," *Kybernetik*, **14**, 4, pp. 241-244, 1974.

The scheme whereby the limit function $\mathscr{L}(x, t)$ (2.55)-(2.56) was derived, as well as the formulations of theorems about the cyclic mean and periodicity in a Leslie model are taken from:

Cull P., Vogt A., "Mathematical analysis of the asymptotic behavior of the Leslie population matrix model," *Bull. Math. Biol.*, **35**, 5/6, pp. 645-661; 1973;

Cull P., Vogt A., "The periodic limits for the Leslie model," *Math. Biosci.*, **21**, 1/2, pp. 39-54, 1974.

For the proofs of the theorem about the total population asymptotic period and of a series of sufficient conditions of periodicity see a note by the same authors:

Cull P., Vogt A., "The period of total population," *Bull. Math. Biol.*, **38**, 3, pp. 317-319, 1976.

To 2.7. Different trends in Leslie matrix model modifications are characterized in the work:

Usher M. B., "Developments in the Leslie matrix model," In: "*Mathematical models in ecology*," Ed. J.N.R. Jeffers, Blackwell, Oxford, pp. 29-60, 1972,

where an extensive bibliography on the subject is provided. Among the later works we shall mention the following:

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—"matrix jump" model;

Cook D., Leon J. A., "Stability of population growth determined by 2×2 Leslie matrix with density-dependent elements," *Biometrics*, **32**, 2, pp. 435-442, 1976;

—an example of modification of (2.77) with inclusion of a dependence on the total population N;

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—an application example of modification of (2.78);

Pip Eva, Stewart J. M., "A method for fitting population data to a matrix model when the growth rate is unknown," *Int. Res. des Hydrobiol.*, **60**, 5, pp. 669-773, 1975;

—other examples of Leslie model applications to natural populations.

To 2.8. A review of results that generalize the Perron-Frobenius theorem for some classes of non-linear eigenvector problems, is presented in the appendix to the monograph by M. Morisima. Unfortunately these results require the functions for system dynamics to be homogeneous to some order, a situation rarely observed in biological populations.

Example (2.89) is taken from the paper:

Beddington J. R., "Age distribution and the stability of simple discrete time population models," *J. Theor. Biol.*, **47**, 1, pp. 65-74, 1974.

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Beddington J. R., Taylor D. B., "Optimum age specific harvesting of a population," *Biometrics*, **29**, 4, pp. 801-809, 1973;

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Mendelsohn R., "Optimization problems associated with a Leslie matrix," *Amer. Natur.*, 110, 973, pp. 339-349, 1976;

as well as in problems of optimal life-cycle evolution:

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Schaffer W. M., Rosenzweig M. L., "Selection for optimal life histories. II. Multiple equilibria and the evolution of alternative reproductive strategies," *Ecology*, 58, 1, pp. 60-72, 1977.

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The dynamic theory of biological populations, Ed. R. A. Poluektov, Nauka, Moscow, 1974 (in Russian).

Relation of the dominating value λ in a Leslie model to the parameters of a continuous model are treated in the paper:

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CHAPTER 3

PREDATOR-PREY TYPE MODELS

3.1. Ecological introduction

One of the first successes of mathematical ecology was the demonstration of population periodic oscillations in a stationary medium. The model created by Volterra for a community in which organisms of one population provided food for those of the other, cleared up the many at first sight incomprehensible phenomena of population periodic change, which in no way could be associated with periodic variations of environmental factors (primarily, climatic ones). Similar phenomena could be observed in communities with one population parasitizing on the organisms of another species.

Communities of such type are usually termed *predator-prey* or *host-parasite* systems.

The biological literature abounds in works where systems are either observed in nature or simulated on "model" populations in laboratory conditions. However, quite often their results are conflicting: some experiments demonstrate oscillations, others lack them; either the system disintegrates quickly enough (the predator dies while the prey remains, or the prey dies and the predator follows suit); or the predator and the prey coexist sufficiently long. Obviously, this fairly simple ecological system is not as simple as it seems. Naturally the question arises: what are the stability conditions of the community, and what mechanisms ensure this stability? In this chapter, using mathematical models of the predator-prey communities, we will try to give an answer to the question.

Another problem is discussed at length. It can be stated as: "Can the predator control the number of prey?" Clearly in a prey population (without a predator) there are some intrinsic internal control mechanisms (for instance, intraspecific competition or epizooties) limiting the population growth. But in this case, if there were no limiting factors (or showed up only at sufficiently large numbers) and the prey population in the absence of the predator grew exponentially, could the influence of the predator stabilize the system as a whole? Do both populations remain limited, and does not one or both of them decline to extinction? Answers to these questions

are the solution of the problem: "Can a predator control the prey number?"

Finally, the last question: "Will random environmental perturbations break down the predator-prey system or will both species remain?" It is considered within the framework of equations for predator-prey system with random perturbations in parameters.

3.2. Classical model of Volterra

Let $x(t)$ and $y(t)$ be the numbers of preys and predators, respectively. Suppose that the only limiting factor for the prey reproduction is the influence of the predator, and the predator reproduction is limited by the amount of hunted food (amount of the prey). Then in the absence of predators the prey population should grow exponentially with a relative rate α, and predators in the absence of the prey should also die out exponentially with a relative rate m. Coefficients α and m are related respectively to the natural birth rate of the prey and the natural death rate of the predator.

Let $V = V(x)$ be the amount (or biomass) of the prey which one predator consumes in a unit time, $1/k$ of the energy consumed with this biomass goes into reproduction of predators, and the rest is spent to sustain metabolism and hunting activity. Then the equation for the predator-prey system can be written in the form

$$\begin{aligned} \frac{dx}{dt} &= \alpha x - V(x)\, y, \\ \frac{dy}{dt} &= y\,[kV(x) - m]. \end{aligned} \tag{3.1}$$

The function $V(x)$ is known as the trophic function or the predator functional response to the prey population density. This is a function usually evaluated in experimental works on preying, and nowadays it is established that they usually belong to one of the following three types (Fig. 11). Apparently, the system dynamic behavior significantly depends on the form of the trophic function.

For small x values, for example, when all the trophic relations in the system are strained and almost all the prey is consumed by the predator, that is always hungry with no saturation (quite a frequent situation in nature), the trophic function $V(x)$ can be taken to be a linear function of the prey population, i.e. $V = \beta x$. Moreover, suppose that $k = \text{const}$. Then

$$\begin{aligned} \frac{dx}{dt} &= \alpha x - \beta xy, \\ \frac{dy}{dt} &= k\beta xy - my. \end{aligned} \tag{3.2}$$

System (3.2) essentially coincides with the classical predator-prey model of Volterra, who showed that this system has an integral of the form

$$\left(\frac{e^X}{X}\right)^m \left(\frac{e^Y}{Y}\right)^\alpha = C, \tag{3.3}$$

where $X = x/x^*$, $Y = y/y^*$, $x^* = m/k\beta$, $y^* = \alpha/\beta$. If x_0 and y_0 are the initial values for the prey and the predator numbers, respectively, then

$$C = \left(\frac{e^{x_0/x^*}}{x_0/x^*}\right)^m \left(\frac{e^{y_0/y^*}}{y_0/y^*}\right)^\alpha > 0$$

and equation (3.3) gives a family of imbedded, closed curves, belonging to phase trajectories of periodic solutions of system (3.2). Notice

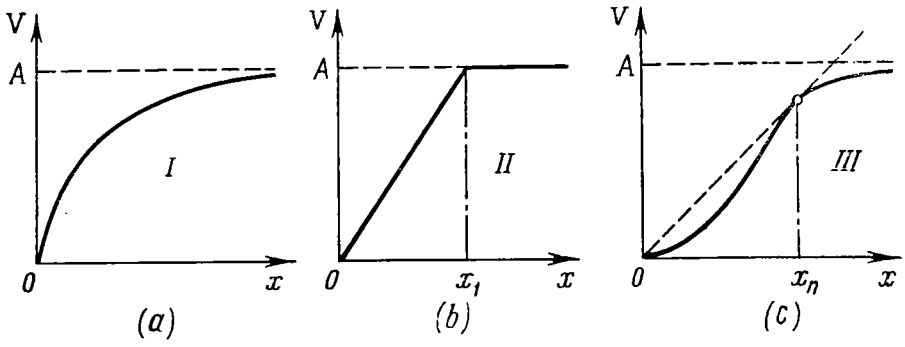

Fig. 11. Different types of trophic functions in the predator-prey system: (a) a type peculiar in invertebrates and some species of fish of prey; (b) the trophic function with a well pronounced saturation threshold specific of filtrator-predators (e.g. most molluscs); (c) a type peculiar in vertebrates, organisms that demonstrate a rather complex behavior (for instance those capable to learn). The trophic function will have a similar form if the prey can develop a defence strategy (for instance find hiding places inaccessible to the predator).

that as C increases, x and y show oscillations of increasing amplitude (Fig. 12). At the minimal value $C^* = e^{(m+\alpha)}$ these curves shrink into a point with coordinates (x^*, y^*). One can easily see that $x^* = m/k\beta$ and $y^* = \alpha/\beta$ are solutions to system (3.2) when $dx/dt = dy/dt = 0$, i.e. its non-trivial equilibrium. For small oscillations about this state ($p = x - x^*$, $q = y - y^*$) the model equations take the form

$$\frac{dp}{dt} = -\frac{m}{k}q, \qquad \frac{dq}{dt} = k\alpha p. \tag{3.4}$$

The roots of the corresponding characteristic equation are $\lambda_{1,2} = \pm i\sqrt{\alpha m}$, that is, the point (x^*, y^*) is a centre. The period of

small oscillations $T = 2\pi/\sqrt{\alpha m}$, and the oscillations of one population with respect to the other are shifted in phase by $\pi/2$.

System (3.2) has another steady state—the origin of coordinates. It is not difficult to see that it is a saddle-point. Coordinate axes are separatrices, and the Oy axis goes into the saddle, while Ox goes out of it (cf. Fig. 12).

Though the Volterra model managed to explain many observed phenomena, it has one great disadvantage—Volterra cycles lack roughness (in the mathematical sense of the word), so that for arbitrarily small perturbations of phase coordinates the system switches from one cycle to another. Apparently, more adequate models should possess this property of "roughness".

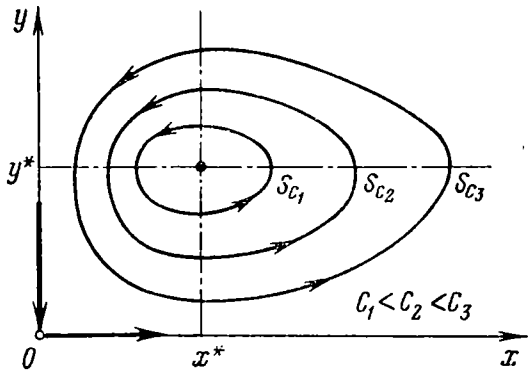

Fig. 12. Phase portrait of the classic Volterra predator-prey system.

From the viewpoint of stability theory, the system steady state (x^*, y^*) is a state of neutral equilibrium, which is stable in Lyapunov's sense, but not asymptotically. The absence of asymptotic stability of equilibrium indicates that the Volterra system has no mechanisms to maintain its non-trivial steady state.

The above statement about equilibrium stability can be easily enough proved by constructing an appropriate Lyapunov function. But this we leave for the next section.

3.3. Predator-prey system stabilization by introduction of intraspecific competition among the prey

Even a simple analysis of the premises of the Volterra model demonstrates their arbitrariness. For instance, without predators the prey population can grow infinitely. In reality this does not happen, because of the limited resources (food, space, etc.) for the population, which restricts its size. On the other hand, the amount of prey consumed by a predator in a unit time can increase indefinitely with increasing prey population, which is not the case too, since there are purely physiological constraints.

The most interesting qualitative conclusion of Volterra as to undamped population oscillations, unfortunately, is a consequence of the specially chosen form of model equations.

It can be shown, for instance, that the introduction of intraspecific competition among the prey, resulting from the limited resources, makes the Volterra model "rough", but the oscillations become

damped. Model equations in this case take the form

$$\begin{aligned} \frac{dx}{dt} &= \alpha x - \beta xy - \gamma x^2, \\ \frac{dy}{dt} &= k\beta xy - my, \end{aligned} \tag{3.5}$$

where the term γx^2 stands for intraspecific competition. It is immediately apparent that in the absence of predators the limit value of the prey population will be $\bar{x} = \alpha/\gamma$. System (3.5) has a unique nontrivial equilibrium at the point (x^*, y^*), where

$$x^* = \frac{m}{k\beta}, \qquad y^* = \frac{\alpha k\beta - \gamma m}{k\beta^2}.$$

The realization of the obvious condition $x^* < \bar{x}$ $(m/k\beta < \alpha/\gamma)$ makes y^* positive, and hence this equilibrium exists. It may be shown that this equilibrium is always stable (asymptotically). For

$$\gamma m (\gamma + 4k\beta) < 4\alpha k\beta \tag{3.6}$$

the point (x^*, y^*) is a focus. (Since a system, with (3.5) as its special case, is thoroughly examined in the next section, all these conclusions are presented here without proof.) The question still remains: is there a stable limit cycle inside the positive quadrant? Let us prove that there is no such cycle, and every trajectory initiating inside the quadrant eventually arrives at the point (x^*, y^*). The last statement actually implies asymptotic stability of this point in any closed domain inside the quadrant. For the proof we set up the appropriate Lyapunov function (notice that for $\gamma = 0$ system (3.5) turns into the classical Volterra system (3.2), therefore all the following speculations will concern (3.5)).

The existence of the integral for (3.2) strongly suggests the use of it as the appropriate Lyapunov function. Let (x^*, y^*) be an equilibrium state in system (3.5). Consider the function

$$L(x, y) = x^* \left(\frac{x}{x^*} - \ln \frac{x}{x^*} - 1\right) + \frac{y^*}{k} \left(\frac{y}{y^*} - \ln \frac{y}{y^*} - 1\right). \tag{3.7}$$

Since for any $z > 0$ the inequality

$$z - 1 \geqslant \ln z$$

is satisfied (the equality is only possible for $z = 1$), one can easily see that everywhere in the positive quadrant of the $\{x, y\}$ plane $L(x, y) \geqslant 0$, and $L = 0$ only at the point (x^*, y^*). Function L has continuous partial derivatives in this domain, while the derivative dL/dt calculated along the trajectory (3.5) equals

$$\frac{dL}{dt} = -\gamma (x - x^*)^2 \leqslant 0. \tag{3.8}$$

Obviously, for $\gamma \neq 0$ the derivative dL/dt is only zero on the line $x = x^*$. The point (x^*, y^*) is the only invariant set on this line. From this immediately follows the asymptotic stability of this point, the stability domain coinciding with the positive quadrant of the $\{x, y\}$ plane. Thus there should be no stable limit cycles inside this quadrant. Because of (x^*, y^*) being a stable focus or a knot, the system (3.5) is "rough" (in terms of Andronov-Pontryagin) in any closed domain inside the quadrant.

If the condition (3.6) holds, oscillations appear in (3.5) at any non-zero initial population values; these oscillations dampen out, and the population numbers approach their equilibriums.

For $\gamma = 0$ (as expected) $dL/dt \equiv 0$ and according to the same Lyapunov's theorems the point (x^*, y^*) is stable, but not asymptotically so, and the stability domain (regarded here as the set for which the Lyapunov function keeps its properties) also coincides with the positive quadrant.

Such a strong relationship between the qualitative behavior of solutions and concrete forms of right-hand sides (in ecology the qualitative level is most common for describing types of interactions, since accurate quantitative relationships are usually impossible to obtain) naturally called for a more general formulation of model description, than was proposed by Volterra.

3.4. General predator-prey model (Kolmogorov model)

The trend for a maximally general description of predator-prey system is most pronounced in the work of A. N. Kolmogorov. He completely rejected the explicit form of species characteristics and of functional relations in interspecific interactions, using only some qualitative assumptions.

When there is no intraspecific competition in the predator population, the Volterra model naturally can be generalized by the model

$$\begin{aligned} \frac{dx}{dt} &= \alpha(x) \cdot x - V(x) \cdot y, \\ \frac{dy}{dt} &= K(x)\, y. \end{aligned} \tag{3.9}$$

Unlike Volterra, Kolmogorov makes no *a priori* assumptions about the particular form of functions α, V, and K—the latter being the coefficient of natural birth-rate for predator.

For these functions to have a biologically sensible interpretation, let us state some qualitative assumptions about their dependence on x.

(a) $\alpha'_x < 0$; $\alpha(0) > 0 > \alpha(\infty)$. These constraints can be interpreted in the following way: in the absence of the predator the prey birth rate coefficient diminishes with increasing population, going

from positive to negative values. In other words, the prey population features an intraspecific competition for a limited resource, so that even without the predator the prey population cannot grow infinitely and is stabilized on the level governed by the equation $\alpha(\bar{x}) = 0$.

(b) $K'_x > 0$; $K(0) < 0 < K(\infty)$. This means that the predator birth rate coefficient increases with the prey population, going from negative (for a lack of food) to positive values.

(c) $V(x) > 0$ at $x > 0$; $V(0) = 0$.

One can easily see that system (3.9) has two or three stationary points in the positive quadrant: point (0, 0); point $(\bar{x}, 0)$ where $\bar{x}$ follows from the equation $\alpha(\bar{x}) = 0$; and point (x^*, y^*) determined from the equations (at $\alpha(x^*) > 0$, i.e. when $x^* < \bar{x}$)

$$\alpha(x^*)\, x^* - V(x^*)\, y^* = 0, \qquad K(x^*) = 0. \tag{3.10}$$

Linearizing (3.9) we can now study the trajectory behavior in the neighborhood of steady state points. Let $p = x - x^0$, $q = y - y^0$, where x^0 and y^0 are the coordinates of these points.

1. At the point (0, 0) we get

$$\frac{dp}{dt} = \alpha(0)\, p, \qquad \frac{dq}{dt} = K(0)\, q. \tag{3.11}$$

The roots of the characteristic equation, $\lambda_1 = \alpha(0)$ and $\lambda_2 = K(0)$, are real and have different signs, thus this point is a saddle. The x and y axes are separatrices, the first one going out of the saddle and the second into it.

2. At the point $(\bar{x}, 0)$ the linearized equations take the form:

$$\frac{dp}{dt} = \alpha'_x(\bar{x})\, \bar{x}p - V(\bar{x})\, q, \qquad \frac{dq}{dt} = K(\bar{x})\, q. \tag{3.12}$$

The roots of the characteristic equation are $\lambda_1 = \alpha'_x(\bar{x})\, \bar{x}$, $\lambda_2 = K(\bar{x})$. Since $\alpha'_x < 0$, $\lambda_1 < 0$. If $K(\bar{x}) > 0$, i.e. $\bar{x} > x^*$, then $\lambda_2 > 0$ and this point is a saddle. The separatrices slopes are $\gamma_1 = 0$, $\gamma_2 = (\lambda_1 - \lambda_2)/V(x^*) < 0$. The separatrix originating from the saddle with the slope γ_2 is directed inwards of the positive quadrant. At $\bar{x} < x^*$, $K(\bar{x}) < 0$, and the point $(\bar{x}, 0)$ is a stable knot.

3. At the point (x^*, y^*) we have

$$\frac{dp}{dt} = -\delta p - V(x^*)\, q, \qquad \frac{dq}{dt} = [K'_x(x^*)\, y^*]\, p, \tag{3.13}$$

where

$$\delta = V'_x(x^*)\, y^* - \alpha'_x(x^*)\, x^* - \alpha(x^*).$$

The characteristic equation for this system has the form

$$\lambda^2 + \delta\lambda + V(x^*)\, K'_x(x^*)\, y^* = 0. \tag{3.14}$$

Since the product of roots $V(x^*) K'_x(x^*) y^*$ is positive, the point (x^*, y^*) is either a focus (for $\delta^2 < 4VK'_x y^*$), or a knot (for $\delta^2 > 4VK'_x y^*$). Stability is determined by the sign of δ (for $\delta > 0$—stability, for $\delta < 0$—instability).

Let us look at the behavior of the separatrix originating from $(\bar{x}, 0)$ into the positive quadrant. Because of our assumptions the trajectories cannot go to infinity (the prey population is limited thereby limit-

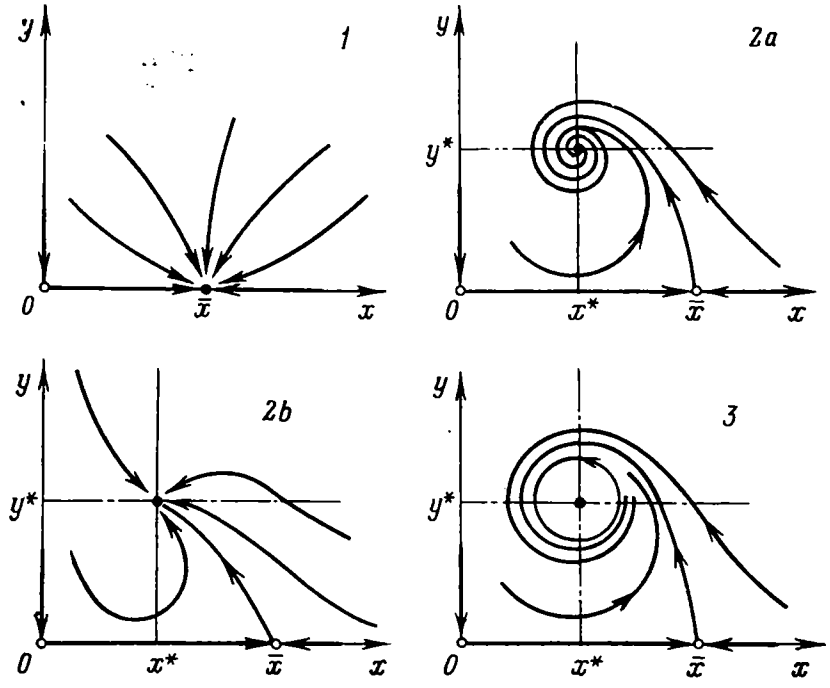

Fig. 13. Different types of phase trajectories in the Kolmogorov model.

ing the predator population preying on it), therefore only the following cases are possible: (1) the separatrix winds around the limit cycle; (2) the separatrix leads to the point (x^*, y^*). Obviously, in the latter case point (x^*, y^*) should be stable.

Eventually, we arrive at the following classification (the corresponding phase trajectories are shown in Fig. 13).

1. $x^* > \bar{x}$, point $(\bar{x}, 0)$ is a stable knot.

2. $x^* < \bar{x}$, the separatrix originated from $(\bar{x}, 0)$ leads to (x^*, y^*); when $\delta^2 < 4V(x^*) K'_x(x^*) y^*$ the point (x^*, y^*) is a stable focus (2*a*); when $\delta^2 > 4V(x^*) K'_x(x^*) y^*$—a stable knot (2*b*).

3. $x^* < \bar{x}$, the separatrix originating from $(\bar{x}, 0)$ winds around a limit cycle Γ; the trajectory behavior inside Γ can be rather complicated and within the framework of our assumptions cannot be completely analyzed.

It can be easily seen that the system (3.5) studied in the preceding section belongs to the second class.

Consider the third class in more detail. If the point (x^*, y^*) is an unstable knot or focus, the system can have a unique limit cycle and it has to be stable by all means. If the point (x^*, y^*) is stable, the unique limit cycle is necessarily semi-stable. Generally, there can be a whole family of cycles around (x^*, y^*), and if one of them is stable, the next one is necessarily unstable.

If we assume the number of limit cycles to be stable, with no semi-stable cycles among them, then the system will be "rough" in any closed domain of the positive quadrant.

The basic result of the undertaken analysis is that we have shown how fairly simple and natural assumptions about the character of inter- and intraspecific interactions lead to quite a complicated behavior in the predator-prey system. And what is the most interesting is that a natural (without special assumptions) existence of a limit cycle is possible in the system.

Here it should be noted, however, that the condition (a) $\alpha'_x < 0$, which is important for our analysis, means nothing but that a self-regulation should be present in the prey population. Therefore the existence of stable non-trivial equilibrium in a predator-prey system owing only to the predator control of the prey population is still open to question. The problem is clarified in the next section.

3.5. Types of predator trophic functions. Predator-prey system stability

The Kolmogorov model makes one essential assumption: it is supposed that $\alpha'_x < 0$ and $\alpha(\bar{x}) = 0$ for $\bar{x} < \infty$, and therefore the prey population has mechanisms to regulate its size even in the absence of predators.

Unfortunately, such a formulation of the model cannot answer the question posed above, which recently gave rise to heated discussion: how can the predator population act as a regulator of the prey to make the whole system stable? Because of this we shall go back to model (3.1) with no self-regulating mechanisms (for instance, regulation through intraspecific competition) in the prey population (as well as in the predator population) however; therefore, the only regulating mechanism for the species populations in the community is the trophic interactions between the predator and the prey.

Now $\alpha = \text{const}$ (so unlike the previous model, $\alpha'_x = 0$). Clearly the solutions to (3.1) depend on the particular form of the trophic function $V(x)$, which in turn is determined by the type of preying, that is, the predator's trophic strategy and the defence strategy of the prey. The following features are in common for all of these

functions (cf. Fig. 11)

$$\text{(a)}\quad V(0) = 0; \qquad \text{(b)}\quad V'_x \geqslant 0; \qquad \text{(c)}\quad V(\infty) < \infty. \tag{3.15}$$

System (3.1) has one non-trivial steady-state point with coordinates that follow from the equations

$$y^* = \frac{\alpha k}{m} x^*, \qquad V(x^*) = \frac{m}{k} \tag{3.16}$$

with the natural restriction $m/k < V(\infty)$.

There is one more steady-state point (0, 0), corresponding to the trivial equilibrium. One can easily show that this point is a saddle, and coordinate axes serve as separatrices.

The characteristic equation for point (x^*, y^*) takes the form

$$\lambda^2 - \lambda\alpha\,[1 - f(x^*)] + \alpha m f(x^*) = 0 \tag{3.17}$$

where

$$f(x) = \frac{V'_x(x)}{V(x)/x}.$$

Clearly, in the classical Volterra model $f(x) \equiv 1$. Therefore the quantity f may be considered as a measure of deviation of the examined model from Volterrian.

When

$$[1 - f(x^*)]^2 < \frac{4m}{\alpha} f(x^*), \tag{3.18}$$

the steady-state point (x^*, y^*) is a focus and the system shows oscillations; if the opposite inequality holds, it is a knot and there are no oscillations in the system. Stability of this equilibrium state is determined by the condition

$$f(x^*) > 1, \quad \text{or} \quad V'(x^*) > V(x^*)/x^*, \tag{3.19}$$

and therefore depends strongly on the form of the predator trophic function.

Condition (3.19) can be interpreted in the following way: for a non-trivial equilibrium in a predator-prey system to be stable (and thus for this system to exist) it is sufficient that the relative fraction of the prey consumed by the predator be increasing with prey population in the neighbourhood of this state. In fact, the fraction of the prey (of its total population) consumed by the predator is characterized by the differentiable function $V(x)/x$, the condition of its growth (positiveness of the derivative) being

$$V'(x)/x - V(x)/x^2 > 0,$$

or

$$V'(x) > V(x)/x.$$

The last condition taken at the point x^* is nothing but the condition (3.19) of equilibrium stability. For $V'(x)$ to be continuous it should also be satisfied in a neighborhood of x^*. Thus, if the prey populations in this neighborhood are $x_1 < x^* < x_2$, then

$$V(x_1)/x_1 < V(x^*)/x^* < V(x_2)/x_2. \tag{3.20}$$

Let the trophic function V now take the form as shown in Fig. 11*a* (which is typical of invertebrates). It can be shown that for all finite values of x (since $V(x)$ is concave)

$$V(x_2)/x_2 < V(x_1)/x_1 \quad \text{for} \quad x_2 > x_1,$$

i.e. for all steady-state prey populations inequality (3.19) does not hold.

This means that a system with such a form of the trophic function has no stable non-trivial equilibrium. Several outcomes are possible: either the populations of both the prey and the predator grow indefinitely, or (when the trajectory passes near one of the coordinate axes) owing to random factors one of the populations dies out. If all the prey dies, in due course the predator dies too, if the predator extincts first, the prey population starts on an exponential growth. The third alternative—the appearance of a stable limit cycle—is impossible, and that can be easily proved.

In fact, the expression

$$\frac{\partial}{\partial x}\left\{\frac{1}{xy}\left[\alpha x - V(x)\,y\right]\right\} + \frac{\partial}{\partial y}\left\{\frac{1}{xy}\left[y\,(kV(x) - m)\right]\right\}$$
$$= \frac{V(x) - V'(x)\,x}{x^2} = \frac{1}{x}\left[\frac{V(x)}{x} - V'(x)\right] \tag{3.21}$$

is always positive in the positive quadrant whenever $V(x)$ has the form as in Fig. 11*a*. Then, according to the Dulack criterion, in this domain there are no closed trajectories and a stable limit cycle cannot exist.

Thus the conclusion can be drawn: if the trophic function has the form as in Fig. 11*a*, the predator effect cannot provide stability to the prey population, and thus to the system as a whole. The system can only be stable in the case the prey population has its own intrinsic control mechanisms, for instance, intraspecific competition or epizooties. This version of regulation was already considered in Sections 3 and 4.

It has been noted before, that such a trophic function type is typical of insect-predators, whose "victims" are normally also insects. On the other hand, the observed dynamics in many natural "predator-prey" type communities, insect species included, demonstrate characteristic oscillations with very big amplitudes and

extremely specific forms. Usually after a period of more or less steady growth (which can be either monotonic or oscillating with increasing amplitude) the population drastically drops (Fig. 14), thereafter the picture recurs. Apparently, such a dynamic behavior of insect-species populations can be related to the system instability at small and average population numbers and to the action of powerful intrapopulational regulators when the numbers become large.

If the predator-prey system comprises species that can demonstrate a sufficiently complex behavior (for instance, predators can learn

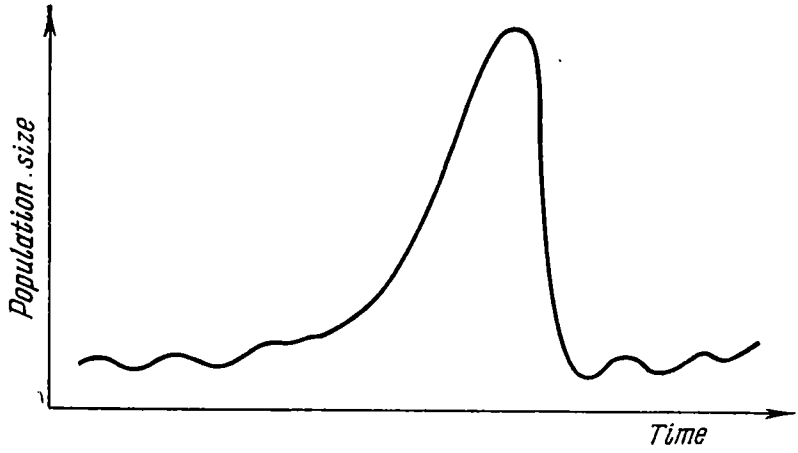

Fig. 14. Population dynamics of *Cardiaspina albitextura* preying on leaves of eucalyptus. (From: Clark L. R., "The population dynamics of *Cardiaspina albitextura*," *Austr. J. Zool.*, **12**, 3, pp. 362-380, 1964).

or preys can find refuge), then such a system may have a non-trivial stable equilibrium. This can be easily proved.

In fact, the trophic function then has to be of the form shown in Fig. 11*c*. The point x_n in the graph is the point where the straight line from the origin is tangent to the curve trophic function $V(x)$. Obviously, the function $W(x) = V(x)/x$ has a maximum at this point. With the same ease it can be shown that for any $x^* < x_n$ condition (3.19) holds. Therefore, the non-trivial equilibrium is asymptotically stable when it is attained at the prey population x^* smaller than x_n. However, we know nothing about the size of stability domain for this equilibrium. For example, if there is an unstable limit cycle, this domain is to be found inside the cycle. Alternatively: the non-trivial equilibrium (3.16) is unstable, but there exists a stable limit cycle; in this case we can also speak about the predator-prey system stability. Since the expression (3.21) can change signs as x varies, when the trophic function is chosen as in Fig. 11*c* (for $x < x_n$, $V'(x) > V(x)/x$, for $x > x_n$, $V'(x) < V(x)/x$), the Dulack criterion does not work here and the existence of limit cycles is open to question.

3.6. On the limit cycles in the predator-prey system

So far there has been found no general method to find the limit cycles. Even for a rather simple system, such as (3.1), we cannot perform a general examination when the choice of the trophic function form is more or less arbitrary. Therefore, we shall somewhat simplify the problem, assuming that the system considered is sufficiently close (in what sense, will become clear below) to the classical Volterra system.

Before turning to the search for limit cycles, let us substitute

$$\tau = \alpha t, \qquad \xi = \ln \frac{x}{x^*}, \qquad \eta = \ln \frac{y}{y^*}, \tag{3.22}$$

where (x^*, y^*) is the non-trivial system equilibrium, given by equations (3.16). Instead of $V(x)$ we shall introduce the function

$$w(\xi) = \frac{V[x(\xi)]}{x(\xi)} \cdot \frac{x^*}{V(x^*)}. \tag{3.23}$$

In the classical Volterra model $V(x) = \lambda x$ and $w(\xi) \equiv 1$. The assumption that the considered model is close to the Volterra one means that $w(\xi)$ can be presented in the form

$$w(\xi) = 1 + \varepsilon\varphi(\xi), \tag{3.24}$$

where ε is a small parameter, and $\varphi(\xi)$ is bounded and has a finite derivative.

The transition from $V(x)$ to $w(\xi)$ and the meaning of the small parameter ε are best explained by referring to Fig. 15. Fig. 15*a* shows the trophic function $V(x)$ of the type as in Fig. 11*c*; x_1^* and x_2^* are the equilibria of the prey population, corresponding to two different values of the m/k ratio. The straight line $V = \lambda x$ belongs to the classical model. Clearly, at sufficiently large x the difference between $V(x)$ and the line λx becomes significant, so that even $V(x)$ and λx are close at small x, we cannot speak about the proximity of trophic functions (and hence the proximity of the two models). But the transition from $V(x)$ to the function $W(x) = V(x)/x$ (cf. Fig. 15*b*) overcomes the difficulty, because for the classical model $W_B = \lambda = \text{const}$, and the difference $W - W_B$ remains bounded for all x $[W(\infty) = 0]$. The transition from $V(x)$ to $W(x)$ and further to $w(\xi)$ is essentially related to the coordinate x^* of the steady-state point. Two steady-state points: x_1^* and x_2^* $(x^* < x_n < x_2^*)$ are shown in Fig. 15*a*. Therefore in Fig. 15*c* two functions $w(\xi)$ are illustrated, belonging to one function $V(x)$, but at two different stationary values x^*:

$$w\left(\xi_1 = \ln \frac{x}{x_1^*}\right), \qquad w\left(\xi_2 = \ln \frac{x}{x_2^*}\right).$$

Obviously, the maxima of these functions define the maximal deviations of $w(\xi)$ from 1, and hence the parameter ε may be estimated in the following way:

$$\varepsilon \sim [\max w(\xi) - 1],$$

or in old variables:

$$\varepsilon \approx \frac{\max\limits_{x} W(x) - W(x^*)}{W(x^*)}.$$

If this variable is sufficiently small, ε is really a small parameter, and the two models are close. Characteristically, ε depends on the

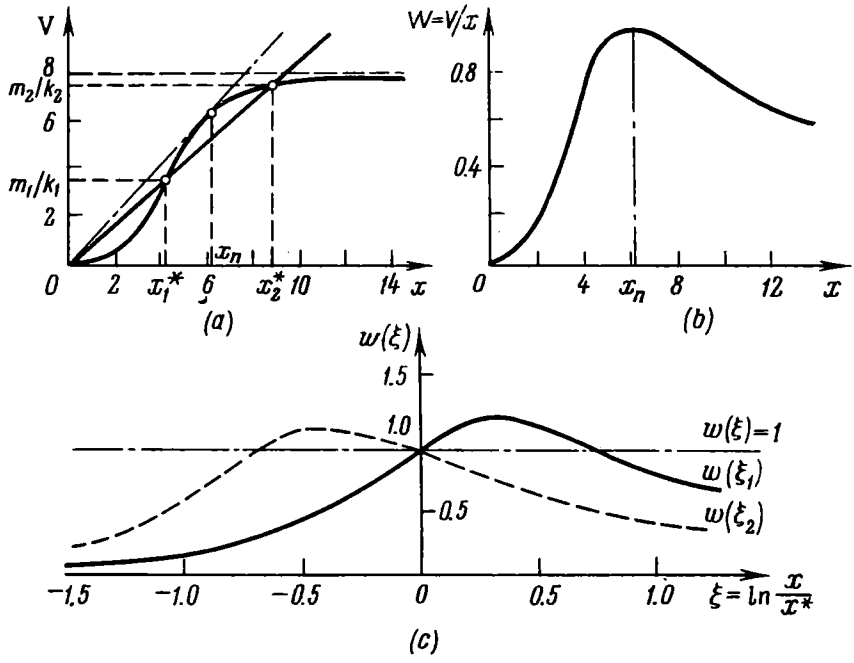

Fig. 15. The transition from $V(x)$ to $w(\xi)$: (a) for the trophic function of a specific form $V(x) = 8x^4/(x^4 + 425)$; (b) $W(x)$ with a maximum at $x_n \approx 6$ is constructed for a given $V(x)$; $W(x) \approx 1$; (c) the functions $w(\xi_1)$ and $w(\xi_2)$ are constructed for two values of the arguments $\xi_1 = \ln(x/x_1^*)$, $x_1^* = 4.3$ and $\xi_2 = \ln(x/x_2^*)$, $x_2^* = 8.8$ belonging to two different steady-state points.

steady state value x^*, i.e. the closeness of model is determined not only by the form of trophic functions, but by all the other parameters as well.

On substituting into (3.1), we get

$$\begin{aligned} \frac{d\xi}{d\tau} &= 1 - w(\xi)\, e^{\eta}, \\ \frac{d\eta}{d\tau} &= \delta\,[w(\xi)\, e^{\xi} - 1], \qquad \delta = \frac{m}{\alpha}. \end{aligned} \tag{3.25}$$

As $\varepsilon \to 0$, system (3.25) becomes classical, which has an integral (in new variables)

$$H = \delta (e^{\xi} - \xi) + (e^{\eta} - \eta).$$

Therefore (3.25) can be written as

$$\begin{aligned} \frac{d\xi}{d\tau} &= -\frac{\partial H}{\partial \eta} - \varepsilon\varphi(\xi) e^{\eta}, \\ \frac{d\eta}{d\tau} &= \frac{\partial H}{\partial \xi} + \varepsilon\delta\varphi(\xi) e^{\xi}. \end{aligned} \tag{3.26}$$

For sufficiently small ε system (3.26) is close to the Hamilton system. For this case Pontryagin has proved a wonderful theorem, which will be now used (see Section 11).

In the plane (ξ, η) the Volterra curves $H(\xi, \eta) = h$ with the centre at (0, 0) are closed. Therefore the line integral

$$\Psi(h) = -\oint\limits_{H(\xi,\eta)=h} \varphi(\xi) e^{\eta} d\eta + \delta\varphi(\xi) e^{\xi} d\xi \tag{3.27}$$

is only determined by the quantity h $(1 + \delta < h < +\infty)$. Then, if there exists such h^* $(1 + \delta < h^* < +\infty)$, that

$$\Psi(h^*) = 0, \qquad \Psi'_h(h^*) \neq 0, \tag{3.28}$$

then there exist positive numbers μ and δ, such that:

(a) for every ε $(|\varepsilon| < \delta)$ system (3.26) has a limit cycle in the μ-vicinity of the curve $H = h^*$, tending to this curve as $\varepsilon \to 0$;

(b) this limit cycle is rough and stable, when $\varepsilon\Psi'_h(h^*) < 0$ and unstable when $\varepsilon\Psi'_h(h^*) > 0$.

The theorem determines only the existence of values of ε, such that the system has a limit cycle; but it gives no estimates.

It would better serve our purposes to consider instead of the line integral (3.27) the equivalent surface integral over the domain S_h, bounded by the Volterra curve $H(\xi, \eta) = h$:

$$\Psi_h = -\iint\limits_{S_h} \varphi'_{\xi}(\xi) e^{\eta} d\xi\, d\eta, \tag{3.29}$$

or in old variables

$$\Psi(C) = -\frac{1}{\alpha} \iint\limits_{S_C} \left[\frac{V(x)}{x}\right]'_x dx\, dy, \tag{3.30}$$

where S_C is the domain delimited by the Volterra cycle (3.3) with the centre at (x^*, y^*).

Obviously, for the condition $\Psi(C_0) = 0$ to hold it is necessary for the derivative of the function $W(x) = V(x)/x$ to change sign on the interval $[x_1, x_2]$, where x_1 and x_2 are the extreme left and

right points of a Volterra cycle. The graphs of the three respective derivatives for the three trophic function types are given in Fig. 16.

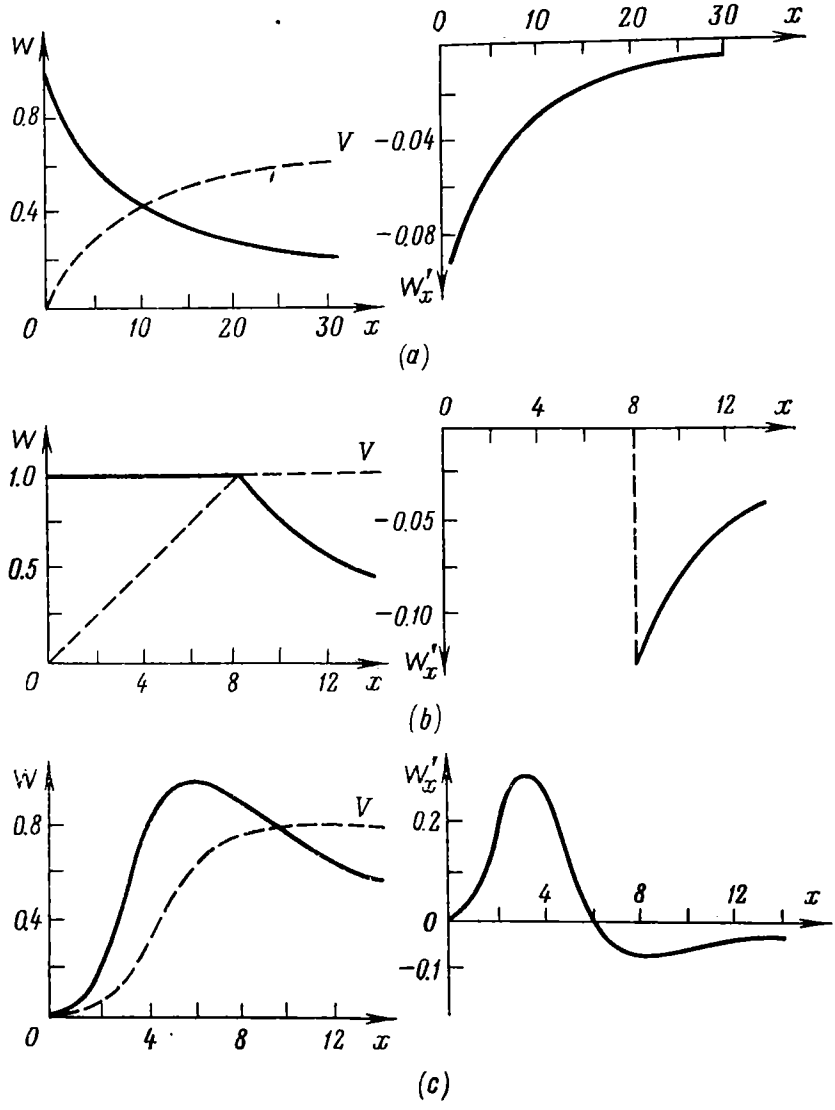

Fig. 16. Three types of trophic functions with appropriate functions $W(x)$ and $W'_x(x)$. These graphs show that only in the case (c) $W'_x(x)$ changes sign as x is varied.

These graphs show that the necessary condition for the existence of a limit cycle is only satisfied for the trophic function as in Fig. 11c*.

* The lack of limit cycles for the functions as in Fig. 11a, b also follows from the Dulack criterion. In fact (cf. Fig. 16a, b),

$$\frac{\partial}{\partial x}\left[\frac{1}{xy}(\alpha x - Vy)\right] + \frac{\partial}{\partial y}\left[\frac{1}{xy}\, y\,(kV - m)\right] = -\left[\frac{V}{x}\right]'_x = -W'_x \geqslant 0.$$

Unfortunately, the above necessary condition is not a sufficient one (we failed to derive the latter in a general form). If we suppose, however, that the desired limit cycle belongs to the immediate vicinity of the steady-state point, the equation of this cycle can be obtained and its stability analysed.

3.7. Non-linear oscillations in predator-prey system

Supposing that the limit cycle belongs to a sufficiently small neighbourhood of a steady-state point, the Volterra cycle can be replaced by an ellipse. Then for small ε system (3.29) should be nearly linear, and as an integral we can take the expression

$$H=\frac{\delta\xi^2}{2}+\frac{\eta^2}{2}=\text{const.} \tag{3.31}$$

Substituting (3.31) for (3.25), we consider the system

$$\begin{aligned}\frac{d\xi}{d\tau}&=-\eta-\varepsilon\varphi(\xi)\,e^{\eta},\\ \frac{d\eta}{d\tau}&=\delta\xi+\varepsilon\delta\varphi(\xi)\,e^{\xi}.\end{aligned} \tag{3.32}$$

To find the asymptotic solution to (3.32), we shall use the Krylov-Bogolubov method. Substituting the variables

$$\xi=a\cos\psi,\qquad \eta=-\sqrt{\delta}\,a\sin\varphi,$$

we can get the equation for a, the amplitude of oscillations in ξ:

$$\frac{da}{d\tau}=-\varepsilon\varphi(a\cos\psi)\,[e^{-\sqrt{\delta}a\sin\psi}\cdot\cos\psi+\sqrt{\delta}\,e^{a\cos\psi}\cdot\sin\psi]. \tag{3.33}$$

Because $a(\tau)$ is a slowly varying function of time, the right-hand side of (3.33) without loss of accuracy can be averaged in phase ψ

$$\frac{da}{d\tau}=\frac{-\varepsilon}{2\pi}\int_0^{2\pi}\varphi(a\cos\psi)\,e^{-\sqrt{\delta}\,a\sin\psi}\cdot\cos\psi\,d\psi, \tag{3.34}$$

since

$$\int_0^{2\pi}\varphi(a\cos\psi)\,e^{a\cos\psi}\cdot\sin\psi\,d\psi=0.$$

As we consider low-amplitude oscillations, the integrand in (3.34) can be expanded as a series in a, neglecting terms of the order of a^4

and higher. Then, considering that $\varphi(0) = 0$, we will have

$$\frac{da}{d\tau} = -\frac{\varepsilon a}{2\pi}\int_0^{2\pi}\left[\varphi'(0)\cos^2\psi + \frac{1}{6}a^2\varphi'''(0)\cos^4\psi + \frac{a^2\delta}{2}\varphi'(0)\sin^2\psi\cos^2\psi\right]d\psi$$

$$= -\frac{\varepsilon a}{2}\left\{\varphi'(0) + \frac{a^2}{8}[\varphi'(0)\delta + \varphi'''(0)]\right\}. \qquad (3.35)$$

The condition $da/d\tau = 0$ provides an equation for the limit cycle in the plane (ξ, η). The limit cycle is an ellipse with semi-axes

$$a^* = \sqrt{\frac{-8\varphi'(0)}{\delta\varphi'(0) + \varphi'''(0)}},$$
$$b^* = \alpha^*\sqrt{\delta}. \qquad (3.36)$$

This cycle is stable if $\delta\varphi'(0) + \varphi'''(0) > 0$, and unstable otherwise. We now immediately obtain the necessary and sufficient conditions for the undamped periodic oscillations (stable limit cycle) in a predator-prey system:

$$\varphi'(0) < 0, \qquad \varphi'(0)\delta + \varphi'''(0) > 0. \qquad (3.37)$$

If sign $[\varphi'(0)]$ = sign $[\delta\varphi'(0) + \varphi'''(0)]$ there is no oscillations in the system.

In order to study the relation between the oscillation character and the system parameters, let us define the trophic function. Let, for instance,

$V(x) = Ax^2/(K + x^2)$ (function as in Fig. 11*c*).

Then

$$w(\xi) = \frac{Ak}{m}\frac{e^{\xi}}{\left(\frac{Ak}{m} - 1\right) + e^{2\xi}},$$

$$\varphi'(0) = 1 - 2b, \qquad \varphi'''(0) = (1 - 2b)(1 - 24b + 24b^2), \qquad (3.38)$$

$$b = \frac{m}{kA}.$$

If we insert (3.38) into (3.35), we get the expression relating the oscillation amplitude to the system parameters α, m, k, and A:

$$a^* = \sqrt{\frac{-8}{1 + m/\alpha - 24b + 24b^2}}. \qquad (3.39)$$

Clearly, the system has a limit cycle if $b_1 < b < b_2$ where

$$b_{1,2} = \frac{1}{2}\left(1 \mp \sqrt{\frac{5\alpha - m}{6\alpha}}\right).$$

Here it is necessary that $5\alpha > m$, i.e. the prey has to multiply rapidly enough, while the predator death-rate is to be small. The cycle is stable at $b > 1/2$ and unstable at $b < 1/2$.

If $0 < b < b_1$, there is no periodic oscillations in the systems, since a is purely imaginary, but there is a steady state at $a^* = 0$ (from (3.35) it follows that $da/d\tau = 0$ when $a = 0$). It is readily seen that this state is stable: $\varphi'(0) = 1 - 2b > 0$. For $1 > b > b_2$ the system also has no periodic stationary solutions, there is one steady state at $a^* = 0$ but it is unstable.

If $b > 1$ $(kA < m)$, the system does not have a single non-trivial equilibrium, be it a stable or unstable one. As $t \to \infty$, $y \to 0$ and $x \to \infty$, i.e. predators die out thereafter the prey population starts to grow indefinitely.

All the above-said can be given the following interpretation. Small values of parameter b belong to small values of m and to large values of k and A, i.e. the predator has a low death rate, a high efficiency of the prey biomass "processing" into its own biomass, and a high saturation level A. In other words, small b values indicate that the predator is well adapted to the biotic, as well as the abiotic, environment. High death rate values, low efficiency and low saturation levels A, i.e. a poorly adapted predator, correspond to large b values*. To all intents and purposes, $1/b$ may be considered as an index of predator adaptation to given environmetal conditions.

What occurs in the system as b grows from 0 to 1? For small b there exists a stable non-trivial equilibrium (knot or focus). If the stable equilibrium at small b is a knot, it might be transformed into a focus when b increases. Lastly, at $b > b_1$ an unstable limit cycle develops in the system to bound the stability domain of the non-trivial equilibrium. When b increases further this domain diminishes. When $b > 1/2$, the unstable cycle becomes stable, and periodic undamped oscillations arise in the system with the amplitude increasing with b. Finally, when $b > b_2$ the stable limit cycle disappears and only the unstable focus or knot is left. In this case, if for $b > b_2$ we had a focus, then as b increases this focus becomes a knot.

Suppose that for small $b \ll b_1$ the system was in equilibrium. Let us slowly (as compared with the effective duration of the transitional processes) increase the parameter b, which corresponds to a slow environment deterioration for the predator. In this case for each value of b we may consider that the system is in a steady state (if any!). There may be two such states—stable equilibrium (stable

* There can also be another interpretation. Let, for instance, the prey be very able to find refuge, or the predator hunting activity be insufficient to catch a good number of prey. Then the trophic function will have a rather low limiting value of A which is also bad for the predator.

steady-state point) and stable oscillations (stable limit cycle). As long as $b < b_{cr}$ the system remains at rest till the critical value $b_{cr} = 1/2$ is attained. On passing this threshold value, the equilibrium becomes impossible, and the system immediately develops oscillations with a finite amplitude. This is the classical situation of "rigid self-exciting" from the theory of non-linear oscillations. As b grows further, the oscillation amplitude increases, but they remain stable till b passes the second threshold value $b = b_2$. After this

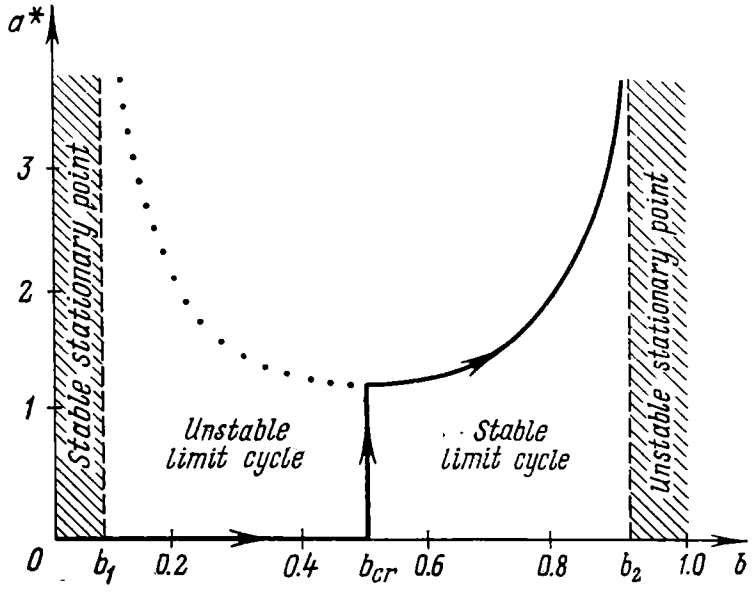

Fig. 17. Variation of the amplitude of stationary oscillations with the parameter b. The solid line shows the behavior of stationary amplitudes as b is slowly increased. It is seen that the predator-prey system is a self-oscillating system with rigid self-excitement.

the oscillations either cease to be stable (the amplitude increases at a fixed b) or disappear completely. There is no steady state in the system. A graphic illustration of this behavior is presented in Fig. 17.

To summarize, it will be recalled that the described behavior should by all means be extended to include the whole phase plane. The Pontryagin method can only be applied to a finite part of the plane, while the domain of our detailed analysis of behavior is still smaller—it is the immediate vicinity of the steady-state point. We have ascertained the existence of at least one limit cycle; however, this cycle is not necessarily unique—it is not inconceivable that other cycles may exist.

3.8. Trajectory behavior at infinity

Because $V(x) \to \text{const} = A$ as $x \to \infty$, in evaluating the predator-prey system behavior at large prey populations, instead of system (3.1) we can look at the approximate system

$$\begin{aligned} \frac{dx}{dt} &= \alpha x - Ay, \\ \frac{dy}{dt} &= y(kA - m) = By. \end{aligned} \tag{3.40}$$

The integral of (3.40) has the form

$$\begin{aligned} x &= Cy^{\alpha/B} + \frac{A}{\alpha - B} y, \qquad \alpha \neq B \\ x &= Cy - \frac{Ay}{\alpha} \ln y, \qquad \alpha = B. \end{aligned} \tag{3.41}$$

After plotting a family of curves (3.41) in the phase plane (Fig. 18),

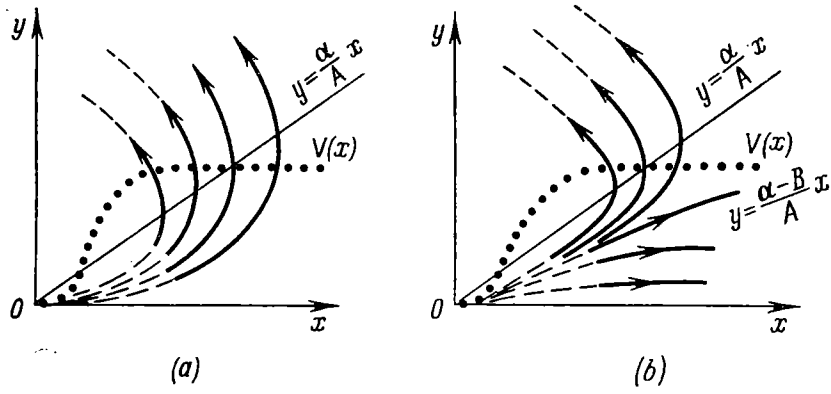

Fig. 18. Phase trajectories for the system (3.40): (*a*) for $\alpha \leqslant B = kA - m$; (*b*) for $\alpha > B = kA - m$. —parts of trajectories for big x such that $V(x) \approx \approx$ const, and system (3.40) is close to system (3.1); - - - the same for small x, when (3.40) cannot be considered close to (3.1); .... the trophic function $V(x)$ given to indicate when x may be considered large.

we can see that the behavior of trajectories of (3.40) differs for $\alpha \leqslant B$ and $\alpha > B$.

Whereas for $\alpha \leqslant B$ $\left(b \leqslant \frac{m}{\alpha + m}\right)$ there is not a single trajectory tending to infinity; but when $\alpha > B$ $\left(b > \frac{m}{m + \alpha}\right)$ such trajectories made their appearance. This result can have the following meaningful interpretation. The maximal birth-rate of the prey is α, of the

predator $(kA-m) = B$. These quantities are known as biotic potentials of the prey and the predator, respectively. So, if the biotic potential of the prey exceeds that of the predator, then at particular initial values the prey population can show a steady infinite growth—the prey population, so to speak, escapes the predator. Equally steadily and infinitely, but at a less rate, grows the predator population. It should be noted that such an "escape" of the prey from the predator is well known in ecology (in insect populations, for instance).

If we now compare the "escape" condition

$$b > \frac{m}{\alpha+m} = \frac{m/\alpha}{1+m/\alpha}$$

with the conditions of the stable limit cycle existence

$$-\frac{1}{2} < b < \frac{1}{2}\left(1+\sqrt{\frac{5}{6}-\frac{m}{6\alpha}}\right),$$

it is readily seen that the domains defined by these inequalities in the plane of parameters b and $\mu = m/\alpha$, overlap (Fig. 19). The presence of such an overlapping seems to suggest the existence of at least one more limit cycle in the system (unstable at that).

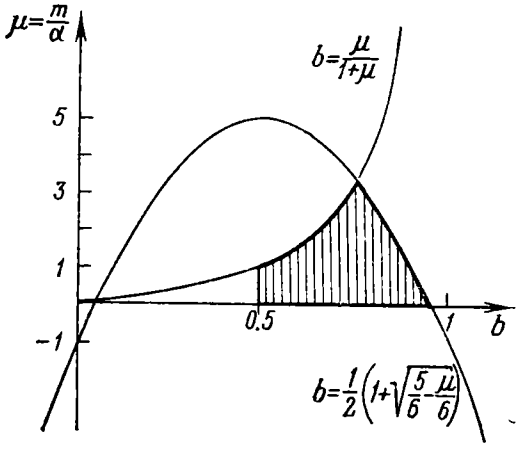

Fig. 19. The "escape" domain with a limit cycle.

Before we leave the subject it is necessary to specify when and in what sense can we speak about the closeness of systems (3.1) and (3.40), at large x. Here it is natural to use the notion of "roughness" (in the sense of Andronov-Pontryagin). Leaving out the details of the proof, we can state that if the domain

$$\Omega = \{(x, y)\colon 0 < x^0 \leqslant x \leqslant C_x < +\infty,\ 0 \leqslant y \leqslant C_y < +\infty\}$$

has no steady-state points of system (3.1), the systems (3.1) and (3.40) are close in the domain Ω. The proximity is considered in the following sense: for every $\varepsilon > 0$ we can find such $\delta > 0$ that if the norm $\| V(x) - A \|$ is less than δ, $\| V'_x(x) \| < \delta$, then $\| (x(t), y(t)) - (\tilde{x}(t), \tilde{y}(t)) \| < \varepsilon$. Here $(x, y), (\tilde{x}, \tilde{y}) \in \Omega$, $t \geqslant 0$, $(x(t), y(t))$ and $(\tilde{x}(t), \tilde{y}(t))$ are the points on the trajectories (3.1) and (3.40).

3.9. Relaxation-type oscillations and ecological catastrophies

Supposing now that there are intra-populational self-regulating mechanisms for the prey population, consider a system of the form

$$\begin{aligned} \frac{dx}{dt} &= \alpha(x)\,x - V(x)\,y, \\ \frac{dy}{dt} &= y\,[kV(x) - m], \end{aligned} \tag{3.42}$$

where $\alpha(x)$ and $V(x)$ allow the following parametrization:

$$\begin{aligned} &\alpha(x) = \alpha_0\,[1-(x/x_S)^p], \qquad p>0, \qquad \alpha_0 = \text{const}, \\ &V(x) = Ax^n/(K^n + x^n), \qquad n>0. \end{aligned} \tag{3.43}$$

Obviously, when $n \leqslant 1$, we get a trophic function of the first type, and when $n > 1$ we get a third-type function. When n increases further the trophic function increasingly exhibits "threshold" behavior. As to the function of intraspecific competition $\alpha(x)$, for $p = 1$ it expresses the logistic law of the prey population growth (in the absence of predator); when $p < 1$ it is the so-called "density-dependent" regulation, and for $p \gg 1$ the regulation is "density-independent" (cf., e.g., Fig. 1*a* from Chapter 1).

Suppose $\alpha_0 \gg 1$, i.e. the prey population reproduces itself much faster than the predator population, which is often the case in nature. Then $1/\alpha_0 \ll 1$, it may be considered a small parameter, and the Tikhonov theorem may be used for an asymptotic study of the system (3.42). But first introduce the dimensionless variables

$$X = x/K, \qquad Y = \frac{Ay}{\alpha_0 K}, \qquad X_S = x_S/K, \qquad b = \frac{m}{kA},$$

and rewrite (3.42) in the form

$$\begin{aligned} \frac{1}{\alpha_0}\frac{dX}{dt} &= X[1-(X/X_S)^p] - Y\frac{X^n}{1+X^n}, \\ \frac{dY}{dt} &= kAY\left[\frac{X^n}{1+X^n} - b\right]. \end{aligned} \tag{3.44}$$

Since $1/\alpha_0 \ll 1$, the structure of the phase portrait of system (3.44) is determined by the shape of the curve

$$Y = \frac{1+X^n}{X^{n-1}}\,[1-(X/X_S)^p], \tag{3.45}$$

which is the non-trivial equilibrium manifold, depending upon the three parameters: X_s, p, n. Clearly, X_s is the carrying capacity

of the environment for the prey species in the absence of predators, and the positive root X^* of the equation $V(X^*) = b$ is the equilibrium prey population. An increment in X_s may be interpreted as an improvement in the environmental adaptation of the prey, and a decrease in X^*, reflecting a decrease in b, an improvement in the adaptation of predators (cf. Section 7). A word about the parameter n is in order. For $n \leqslant 1$ the trophic function belongs to the first type ("stupid" predator), whereas for $n > 1$ it is of the third type ("clever" predator), therefore an increase in n may be regarded as an adaptational improvement in the predator hunting strategy.

Consider the system behavior for different values of the parameter n.

A. Let $n < 1$ (the case of $n = 1$ results in nothing principally new and will not be analyzed separately), i.e. the predator employs a primitive trophic strategy. Curve (3.45) has roots $X = 0$ and $X = X_s$, and it may be shown that for any rational values of n and p ($p > 0$, $0 < n \leqslant 1$) there is exactly one maximum for the curve (3.45) within the interval of these two roots (Fig. 20). From initial states, which lie above the $OA\infty$ curve, the system approaches rapidly (i.e. during a period of time of the order of $1/\alpha_0$) to the OY-axis, i.e. to fast extinction of the prey, after which the predator dies out exponentially (the typical path of the system in this space being $P_1 \to Q_1 \to 0$).

If the initial points lie below the $OA\infty$ branch, different regimes are possible. When $X^* > X_s$, $Y(X^*)$ becomes negative, i.e. the equilibrium (X^*, Y^*) has no ecological meaning. The fate of trajectories is as follows (see Fig. 20*a*): fast dynamics of $X(t)$ leads the system to the equilibrium manifold along which $Y(t)$ decreases slowly to zero, and $X(t) \to X_s$ as $t \to \infty$. When $X_{\max} < X^* < X_s$, there appears a stable equilibrium (X^*, Y^*) of the focus type (not shown in the figure). With $X^* < X_{\max}$, the equilibrium X^* is unstable and a "catastrophe" occurs in the system: a rather long evolution along the X_sA branch of the manifold, when reaching point A, ends with a breakdown, i.e. $X(t)$ tends to zero quickly, thereafter $Y(t)$ tends to zero slowly (the regime also typical for initial states above the $OA\infty$ curve). From an ecological standpoint, this type of trajectory behavior means that a high level of the predator environmental adaptation (i.e. low natural mortality, high efficiency of prey utilization, etc.) eventually leads to the "catastrophe", namely to loss of the prey species and then to extinction of the predator, although the system can persist for a long time.

B. Let the predator employ a more perfect strategy, i.e. $n > 1$ (S-shaped curve, or "type 3" functional response). Within the interval $(0, X_s)$, curve (3.45) is already more complex than in the case in which $n \leqslant 1$; but when $X^* \geqslant X_s$, as before, $Y(t) \to 0$ and $X(t) \to X_s$ (stable dynamics of preys without predators).

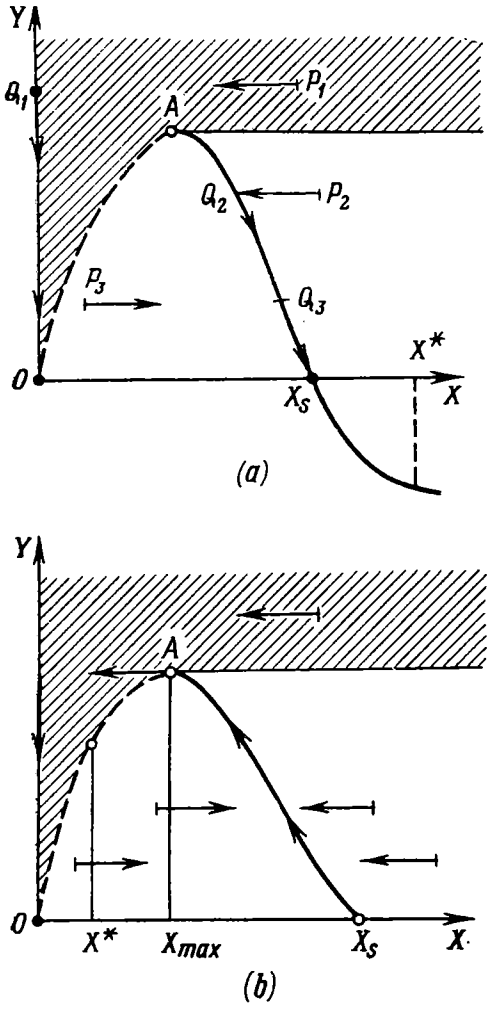

Fig. 20. Phase portraits for system (3.49): $n < 1$.

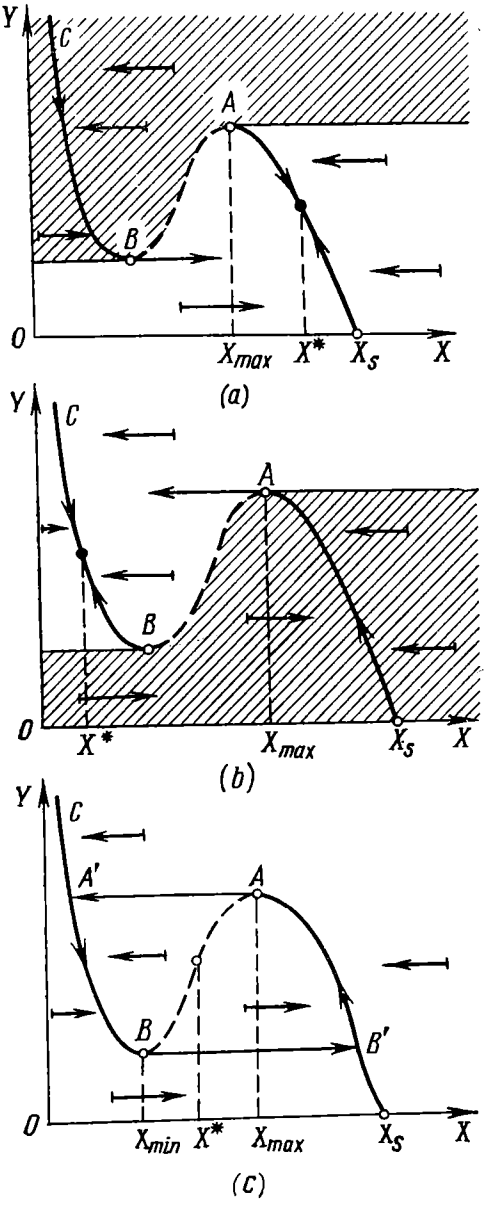

Fig. 21. Phase portraits for system (3.49): $n > 1$.

When $X^* < X_s$, other types of behavior are possible. Let, for instance, the prey species be poorly adapted to the environment, i.e. "carrying capacity" X_s is sufficiently small. More rigorously, let

$$X_s < \begin{cases} p(n-1)^{(p-1)/n}, & \text{if } n < p, \\ 1, & \text{if } n \geqslant p. \end{cases} \tag{3.46}$$

Then the behavior is rather simple: there exists a stable equilibrium (X^*, Y^*) which is reached by the fast passage to the equilibrium manifold and slow movement along the manifold.

Another situation appears with a high degree of prey adaptation, strictly speaking when X_s satisfies the inequality opposite to (3.46). In that case, curve (3.45) has two local extrema within the interval (0, X_s) (see Fig. 21). If the predator adaptation is not too high (i.e. $X^* > X_{\max}$), then there exists a stable equilibrium (X^*, Y^*) with a rather large prey population X^*.

However, more interesting behavior of the system occurs when a trajectory originates from the shaded domain in Fig. 21*a*. The system quickly reaches the branch CB, then moves slowly along it to the point B, makes the "catastrophic" fast jump (in the prey number) to branch AX_s, along which the system moves slowly to the equilibrium.

A similar picture also appears with a high degree of predator adaptation when $X^* < X_{\min}$ (see Fig. 21*b*). From the shaded domain, the system moves quickly to branch AX_s, along which it moves up slowly to the point A, where it makes a "catastrophic" jump down to the branch CB, along which the system moves slowly to the equilibrium (X^*, Y^*).

Finally, the most interesting regime occurs for moderate values of the predator adaptation, i.e. when $X_{\min} < X^* < X_{\max}$ (Fig. 21*c*). The equilibrium (X^*, Y^*) is unstable, but around it there exists a stable limit cycle $AA'BB'$. One may easily imagine the appropriate prey and predator trajectories along the times axis. These are oscillations of a relaxation type with sharp jumps in the prey population against the background of fairly smooth dynamics of the predator. These sharp slumps and climbs are apparently catastrophic in the sense of topological catastrophe theory, since the jumps take place here from one branch of the equilibrium manifold to another. But the above qualitative analysis is clearly insufficient to dub them catastrophes in the ecological sense: in any case the sharp jumps do not result in death of the prey, and only a more reasonable model can show whether or not the outbreaks of the prey population will be catastrophic.

Besides, we may remark that, in contrast to the case of $n \leqslant 1$, when $n > 1$, i.e. when the predator employs a more perfect trophic strategy, there are no phase domains where the system dies out.

3.10. Behavior of predator-prey system in random environments

Random environmental variations usually cause random variations in system parameters, in particular, in the natural growth coefficient of the prey, α, and in the natural mortality of the predator, m. Mathematically, the problem boils down to the study of behavior of the non-linear oscillator, described in the preceding sections, with random oscillations of its parameter. Here arises the problem of parametric resonance regimes; the Krylov-Bogolyubov method provides a fairly good tool for their study. This problem has not yet been solved and still awaits its researcher. We shall consider a more simple problem of the behavior of a linearized system in a small neighborhood of a steady state.

Let the predator-prey system be described by equations (3.5). This means that the prey population is self-regulated (by intraspecific competition), and the system itself may have a stable non-trivial equilibrium (x^*, y^*). Linearizing (3.5) about this state, we get

$$\begin{aligned} \dot{p} &= -x^*(\gamma p + \beta q), \\ \dot{q} &= k\beta y^* p \end{aligned} \tag{3.47}$$

$$\left(p = x - x^*, \quad q = y - y^*, \quad x^* = m/k\beta, \quad y^* = \frac{\alpha k\beta - \gamma m}{k\beta^2}\right),$$

or after the substitution $mt = \tau$, $r = -x^*(\gamma p + \beta q)/m$:

$$\begin{aligned} \frac{dp}{d\tau} &= r, \\ \frac{dr}{d\tau} &= -\nu r - \omega^2 p \end{aligned} \tag{3.48}$$

$$(\nu = \gamma/(k\beta), \qquad \omega^2 = \alpha/m - \nu).$$

It is readily seen that from the condition that $y^* > 0$ it follows that $\omega^2 > 0$. Suppose that the parameter α/m, which depends upon the coefficients of the prey natural growth and the predator natural mortality, may be represented in the form

$$\frac{\alpha}{m} = \frac{\alpha_0}{m_0}[1 + z(\tau)],$$

where α_0/m_0 is the parameter value in the absence of random perturbations, and $z(\tau)$ is a certain random process, chosen not only because of its simplicity, but also because it reflects, to a certain extent, the real-life situations.

Suppose that the characteristic time-scale for the variations of external conditions is τ_0. Over this time period the environmental

conditions may be thought of as constant. The values of the parameter α/m, characterizing the environmental conditions on this interval, we shall regard as the realization of some random variable, distributed normally with the mean $M(\alpha/m) = \alpha_0/m_0$ (then $M(z) = 0$) and the variance $D(\alpha/m) = \frac{\alpha_0^2}{m_0^2}\sigma_0^2$ $[D(z) = \sigma_0^2]$. On the next interval the value of α/m is again the realization of this random variable, and the new realization is by no means related to that of the previous interval. Then if we consider the system behavior within the interval $[0, T]$ and $\tau_0 \ll T$, then the so-called "delta-correlated" Gaussian process with zero mean and the covariance $K_2(\tau_1, \tau_2) = \sigma_0^2\delta(\tau_1 - \tau_2)$, may be chosen as a statistical model for $z(\tau)$. Here δ denotes the delta-function.

We are concerned with the behavior of statistical characteristics of the solution to (3.48), and in particular with dynamics of the moments $\langle p\rangle$, $\langle r\rangle$, $\langle p^2\rangle$, $\langle pr\rangle$, and $\langle r^2\rangle$. (The symbol $\langle\ldots\rangle$ stands here for the operation of averaging over an ensemble of realizations for z.) But before we go on to tackle this problem, make the following change of variables in (3.48):

$$P(\tau) = p(\tau)\,e^{\nu\tau/2}, \qquad Z = \frac{\alpha_0}{m_0\Omega^2}\,z, \qquad \Omega^2 = \omega_0^2 - \frac{\nu^2}{4},$$

$$R(\tau) = [r(\tau) + \nu p(\tau)/2]\,e^{\nu\tau/2}.$$

If the coefficient of intraspecific competition is small enough, then $\omega_0^2 > \nu^2/4$ and $\Omega^2 > 0$. In this case in place of (3.48) we get

$$\begin{aligned} \frac{dP}{d\tau} &= R, \\ \frac{dR}{d\tau} &= -\Omega^2 P - \Omega^2 ZP. \end{aligned} \tag{3.49}$$

Without loss of generality the initial conditions may be given in the form

$$P(0) = 0, \qquad R(0) = 1.$$

Applying the averaging operation to (3.49) we get

$$\begin{aligned} \frac{d\langle P\rangle}{d\tau} &= \langle R\rangle, \\ \frac{d\langle R\rangle}{d\tau} &= -\Omega^2\langle P\rangle - \Omega^2\langle ZP\rangle, \end{aligned} \tag{3.50}$$

and for the second moments

$$\begin{aligned} \frac{d}{d\tau}\langle P^2\rangle &= 2\langle PR\rangle, \\ \frac{d}{d\tau}\langle PR\rangle &= -\Omega^2\langle P^2\rangle + \langle R^2\rangle - \Omega^2\langle ZP^2\rangle, \\ \frac{d}{d\tau}\langle R^2\rangle &= -2\Omega^2\langle PR\rangle - 2\Omega^2\langle ZPR\rangle \end{aligned} \tag{3.51}$$

with the initial conditions

$$\langle P(0)\rangle = 0, \qquad \langle R(0)\rangle = 1, \qquad \langle P^2(0)\rangle = \langle P(0)\,R(0)\rangle = 0.$$

Systems (3.50) and (3.51) are not closed with respect to the moments, since they involve new unknown functions $\langle ZP\rangle$, $\langle ZP^2\rangle$, $\langle ZPR\rangle$, which are the correlations between the random variable Z and the solutions to the system (3.49) or the functions of these solutions. And these solutions, in turn, are functions of Z. However, in the case of the delta-correlated Gaussian process these correlations split.

Let us cite without deduction one important formula from the theory of random processes:

$$\langle Z(\tau)\,\Phi[Z]\rangle = \frac{1}{2}\sigma^2\left\langle\frac{\delta\Phi[Z]}{\delta Z(\tau)}\right\rangle. \tag{3.52}$$

Here $\Phi[Z]$ is a functional of Z, $\delta\Phi/\delta Z$ is its variational derivative, $Z(\tau)$ is a delta-correlated process with $K_2(\xi) = \sigma^2\delta(\xi)$, $\xi = \tau_2 - \tau_1$. In our case $\sigma^2 = \left(\frac{\alpha_0}{m_0-\Omega^2}\right)^2\sigma_0^2$. Therefore

$$\begin{aligned}
\langle ZP\rangle &= \frac{1}{2}\sigma^2\left\langle\frac{\delta P}{\delta Z}\right\rangle,\\
\langle ZP^2\rangle &= \sigma^2\left\langle P\frac{\delta P}{\delta Z}\right\rangle,\\
\langle ZPR\rangle &= \frac{1}{2}\sigma^2\left(\left\langle P\frac{\delta P}{\delta Z}\right\rangle + \left\langle R\frac{\delta P}{\delta Z}\right\rangle\right).
\end{aligned} \tag{3.53}$$

Since the process is delta-correlated, the statistical relationships $P[Z]$ and $R[Z]$ are determined by the relationships between Z and the time derivatives of these variables. Omitting the details of the proof, we can write

$$\frac{\delta P}{\delta Z} = \frac{\partial P'_\tau}{\partial Z} = 0, \qquad \frac{\delta R}{\delta Z} = \frac{\partial R'_\tau}{\partial Z} = -\Omega^2 P. \tag{3.54}$$

Finally, by (3.53) and (3.54), the systems of equations (3.50) and (3.51) may be presented in the form

$$\frac{d\langle P\rangle}{d\tau} = \langle R\rangle, \qquad \frac{d\langle R\rangle}{d\tau} = -\Omega^2\langle P\rangle; \tag{3.55}$$

$$\begin{aligned}
\frac{d\langle P^2\rangle}{d\tau} &= 2\langle PR\rangle,\\
\frac{d\langle PR\rangle}{d\tau} &= -\Omega^2\langle P^2\rangle + \langle R^2\rangle,\\
\frac{d\langle R^2\rangle}{d\tau} &= -2\Omega^2\langle PR\rangle + \sigma^2\Omega^4\langle P^2\rangle.
\end{aligned} \tag{3.56}$$

If the solution to (3.55) coincides with the solution to (3.49) in the absence of random fluctuations, then the solution to (3.56) contains

terms increasing with time (such as $\exp\{\frac{1}{2}\sigma^2\Omega^2\tau\}$ when $\sigma^2\Omega \ll 1$). Returning to the variables p and r, it may be said that the moments $\langle p^2\rangle$, $\langle pr\rangle$ and $\langle r^2\rangle$ are to increase with time, if $\sigma^2\Omega^2 > 2\nu$ or

$$\frac{\alpha_0^2\sigma_0^2}{m_0^2[(\alpha_0/m_0-\nu)-\nu^2/4]} > 2\nu. \tag{3.57}$$

This means that when condition (3.57) is satisfied the system demonstrates statistical parametric shatter as a result of fluctuating environmental conditions, and the equilibrium, which is stable in the absence of these fluctuations, becomes unstable.

With small ν the expression (3.57) may be written in the form

$$\frac{\alpha_0}{m_0}\sigma_0^2 > 2\nu,$$

hence a parametric shatter may occur not only for high-amplitude fluctuations, but also for, say, a high fertility of the prey, or low natural mortality of the predator. In the classic model ($\nu = 0$) a parametric shatter always takes place, i.e. one may say that an equilibrium state of the classic model is always statistically unstable.

3.11. Conclusion. Ecological interpretations

The analysis of the classical model of the predator-prey system and its different generalizations enable the results to be interpreted in the following way.

Despite the numerous drawbacks of the classical model, it mirrors such an important (for the populational ecologist) feature as the population oscillations induced by endogenous factors only. Besides, this model provides a basis for further generalizations. It does not, however, account for the factors responsible for stability of such systems in nature.

The inclusion of intraspecific competition both among the prey and the predator leads to the appearance of a non-trivial stable equilibrium in the model, but stable limit cycles are still impossible in this model, though the phenomenon is observed in nature. Moreover, in principle, the classic model cannot answer the question that caused much argument: "Can the predator regulate the prey population and thus ensure stability of the whole system?" For this reason we have looked at a class of models different from the classic one only in that the form of the trophic function may be chosen more arbitrarily.

It turned out that for an S-shaped function the above question may be answered positively. What is more, stable limit cycles appear in such a model.

It would be interesting to know, how the system behavior is affected when the environmental conditions are impaired (for the predator), the fertility of the prey is enhanced or some new defence strategies are employed. If originally the system had no non-trivial stable equilibria and produced no oscillations, the impairment first results in damped oscillations; though stability of the non-trivial equilibrium is preserved, the stability domain is reduced—the predator already fails to regulate the predator population in any domain of the phase plane. Next the oscillations become undamped—a stable limit cycle emerges, these oscillations appearing suddenly ("rigid self-excitation"). When the degree of predator adaptation is further reduced, the system possibly cannot display any stable equilibria or stationary oscillations, and the predator can no longer regulate the prey population, thus the system loses stability. When the prey fertility is enhanced the "escape-effect" appears in the system, again resulting in the loss of stability.

Random environmental fluctuations above all result in a reduction of the stability domain of the non-trivial equilibrium in the space of parameters. In this case, the reason for the loss of stability is the parametric shatter.

Increase in the prey fertility results in the reduction of the stability domain both in the space of parameters and the phase space. In other words, if the prey natality is high, then the reserve of stability in such a system is small and the predator (with a low degree of adaptation) cannot provide regulation of the prey population and thereby the stability of the whole system.

3.12. Notes and bibliography

To 3.1. There is a great body of literature concerned with population dynamics for two species, interacting in the predator-prey manner; these works incorporating the results of observations both in natural systems and in artificially constructed laboratory systems. The most well-known are the observations made for the variations of the lynx and hare populations in Canada (over a period of about a hundred years), and the laboratory experiments of G. Gause carried out in the 1930's for two populations of protozoa. Among the rather recent works we can mention the extensive experiments by Utida:

Utida S., "Cyclic fluctuations of population density intrinsic to the host-parasite system," *Ecology*, 38, 3, pp. 442-449, 1957.

He performed several dozens of experiments, but nevertheless failed to discover a kind of general regularity in the behavior of the host-parasite system, except maybe for the presence of oscillations in the populations and a phase shift. Some of the experimental systems died out quickly, others persisted for rather long periods of time and the oscillations smoothed out.

Quite recently there appeared a series of works focusing on the study of different regulation mechanisms for the prey population in these systems (among them, the mechanisms related to the species spatial distribution and their behavioral reactions):

White E. G., Huffaker C. B., "Regulatory processes and populational cyclity in laboratory populations of *Anagasta kuhniella*. II. Parasitism,

predation, competition and protective cover," *Res. Pop. Ecol.*, **11**, 2 pp. 150-155, 1969;
Matsumoto B. M., Huffaker C. B., "Regulatory processes and population cyclicity in laboratory populations of *Anagasta kuhniella*. V. Host finding and parasitization in a "small" universe by an entomophagous parasite, *Venturia canescens*," *Res. Pop. Ecol.*, 1974, **15**, pp. 193-212; VI. Host finding and parasitization in a "large" universe by an entomophagous parasite, *Venturia canescens*," *Res. Pop. Ecol.*, 1974, **15**, pp. 213-234.

In the work:

Pimental D., "Population regulation and genetic feedback," *Science*, 159, 3822, pp. 1432-1437, 1968,

a new explanation for the mechanism of stability formation in the host-parasite system is suggested on the basis of genetic coevolution of the two populations. These kinds of model, however, lie beyond the framework of our presentation.

To 3.2. The notion of the functional response (trophic function) was first introduced by Holling in his famous experimental works on the predation:

Holling C. S., "The functional response of predator to prey density and its role in mimicry and population regulation," *Mem. Entomol. Soc. Canada*, 45, pp. 1-60, 1965.

In Holling's work the S-shaped trophic functions were obtained under severe restrictions on the predator ration. However, Royama in his work:

Royama T. A., "A comparative study of models of predation and parasitism," *Res. Pop. Ecol.*, Supp. 1, pp. 1-91, 1971,

showed that these restrictions may be released. And eventually the paper

Hassel M. P., Lawton J. H., Beddington J. R., "Sigmoid functional responses by invertebrate predators and parasitoids," *J. Anim. Ecol.*, 46, 1, pp. 249-262, 1977,

gives a long body of experimental evidence suggesting that it is precisely the S-shaped trophic function which is most widespread in real natural systems, and not only among vertebrates but also among invertebrate predators and parasites.

However, there are experiments which produced trophic functions of quite an exotic shape; for instance, an infinitely growing function with a number of changes in its sign of curvature. See, e.g.,

Haynes D. L., Sisojevic P., "Predator behavior of *Philodromus rufus Walckenaer*," *Can. Entomol.*, 98, 1, pp. 113-133, 1966.

To 3.3. Here we used the well-known theorem of Barbashin-Krasovsky about stability on the whole, or global stability:

Barbashin E. A., "Introduction to stability theory," Nauka, Moscow, Chapter 1, 1967 (in Russian).

For the notion of "roughness" for dynamic systems, see, for instance,

Bautin N. N., Leontovich E. A., "Methods and techniques of qualitative study of dynamic systems in the plane," Nauka, Moscow, 1976 (in Russian).

To 3.4. A generalization for the Volterra model was first suggested by A. N. Kolmogorov in the paper:

Kolmogorov A. N., "Sulla teoria di Volterra della lotta per l'esistenze," *G. Inst. Ital. Attuari*, 7, 1, pp. 74-80, 1936.

A revised and complemented variant of this work is:

Kolmogorov A. N., "Qualitative analysis of mathematical models of populations," Nauka, Moscow, pp. 100-106, 1972 (*Problems of cybernetics*; Vol. 25). (in Russian).

Similar models were considered in the papers:

Rosenzweig M. L., MacArthur R. H., "Graphical representation and stability conditions of predator-prey interactions," *Amer. Natur.*, 97, 893, pp. 209-223, 1963;

Rescigno A., "The struggle for life: 1. Two species," *Bull. Math. Biophys.*, 29, 2, pp. 337-388, 1967.

Clearly, the Kolmogorov model with its wide spectrum of different phase trajectories could give a qualitative description of practically any real situation, but the excess of generality presents difficulties in both the quantitative identification of the model and the interpretation of the results obtained. For this reason there appeared quite a lot of models, which may be placed somewhere between the Volterra and Kolmogorov model. To some extent the above-cited model of Rosenzweig and MacArthur is also of this kind. In terms of our notations it has the form

$$\frac{dx}{dt}=\alpha(x)\,x-V(x)\,y, \qquad \frac{dy}{dt}=y\,[kV(x)-m].$$

It was studied in more detail by Freedman:

Freedman H. I., "Graphical stability, enrichment and pest control by a natural enemy," *Math. Biosci.*, 31, 3/4, pp. 207-225, 1976,

who obtained the stability conditions for the non-trivial equilibrium. But the most interesting of his results are the sufficient conditions for the limit cycle to exist.

Different types of behavior of phase trajectories for the trophic function I under self-regulation in either the prey population or the predator population, or both, were given a detailed treatment in the paper:

Bazykin A. D., "The Volterra system and the Michaelis-Menten equation," In: "*Problems of mathematical genetics*," Novosibirsk, Siberian Branch of the Acad. Sci. USSR, pp. 103-143, 1974 (in Russian).

Self-regulation was described by terms of the form $-\gamma_x x^2$ and $-\gamma_y y^2$.

To 3.5. A model of this type [$\alpha(x)$ = const] was first suggested in the work:

Gause G. F., Smaragdova N. P., Witt A. A., "Further studies of interaction between predator and prey," *J. Anim. Ecol.*, 5, 1, pp. 1-18, 1936,

and used to interpret the experiments of Gause in laboratory predatory-prey systems.

To 3.6. In the cited paper by Freedman, and also in the works:

Freedman H. I., Waltman P., "Perturbation of two-dimensional predator-prey equations," *SIAM J. Appl. Math.*, 28, 1, pp. 1-10, 1975;

Freedman H. I., Waltman P., "Perturbation of two-dimensional predator-prey equations with an unperturbed critical point," *SIAM J. Appl. Math.*, 29, 4, pp. 719-733, 1975,

for systems close to those of Volterra, that is for systems of the form

$$\frac{dx}{dy}=\alpha x-\beta xy-\varepsilon f_1(x,\ y)$$

$$\frac{dy}{dt}=k\beta xy-my-\varepsilon f_2(x,\ y),$$

sufficient conditions were derived under which there exists a stable limit cycle. Generally speaking, they follow immediately from the Hopf bifurcation theorem; see, e.g.,

Cesari L., *Asymptotic behavior and stability problems in ordinary differential equations*, Springer-Verlag, Berlin, 1959,

but they appear so cumbersome, that even to check them is a rather complicated problem. Besides, it is hard to find a meaningful interpretation for the small parameter ε. For instance, if the trophic function $V(x)$ is bounded, then for sufficiently big x, $V(x)$ will differ notably from the linear function $v_v=\beta x$ which is the trophic function in the Volterra model. At the same time if we switch to variables $(\xi,\ \eta)$, then the notion of proximity becomes quite evident and a graphic interpretation for the small parameter becomes possible. The

Pontryagin theorem enables us to obtain existence conditions for a stable limit cycle in a simple and biologically meaningful form.

The Pontryagin theorem cited here was first presented in the paper

Pontryagin L. S., "On dynamic systems close to the Hamilton systems," *JETP*, 4, 8, 1934 (in Russian).

To 3.7. For the Krylov-Bogolubov method see, for instance,

Moiseev N. N., *Asymptotic methods in non-linear mechanics*, Nauka, Moscow, 1969 (in Russian).

Note that a similar solution could be derived directly from (3.29) or (3.30) by taking for S_h (or S_c) an ellipse and expanding the integrand as a Taylor series retaining the appropriate powers. Since h^* (or C^*) may be expressed in terms of the lengths of semi-axes in the ellipse, the equation $\psi(h^*) = 0$ [$\psi(C^*) = 0$] is nothing but an equation for stationary amplitudes.

The concrete representation of the type III trophic function in the form

$$V(x) = \frac{Ax^2}{K + x^2}$$

was suggested in the work:

Hassel M. P., Varley G. C., "New inductive population model for insect parasites and its bearing on biological control," *Nature*, **223**, 5211, pp. 1133-1137, 1969.

To 3.8. The really observed "escape-effect" in the predator-prey system for two insect populations was described in the paper:

Takanashi F., "Reproduction curve with two equilibrium points: a consideration on the fluctuation of insect population," *Res. Pop. Ecol.*, **6**, 1, pp. 28-36, 1964.

To 3.9. In this section we basically follow the work

Logofet D. O., Svirezhev Yu. M., "Ecological modeling, catastrophe theory and some new concepts of stability," *Euro-IFIP* 79, North-Holland Publ. Co., Amsterdam, N.Y., Oxford, 1979, pp. 287-293.

A useful introduction to the field of applications of the topological catastrophe theory in models of population dynamics may be found in the paper

Jones D. D., "The application of catastrophe theory to ecological systems," *IIASA Report RR*-75-15, Laxenburg, Austria (June 1975).

To 3.10. For the application of the Krylov-Bogolyubov method in the search for a parametric resonance in non-linear oscillating systems with random parameters see:

Mitropolsky Yu. A., *Averaging method in non-linear mechanics*, Naukova Dumka, Kiev, 1971 (in Russian).

The techniques utilized in this section is presented in the book:

Klyatskin V. I., *Statistical description of dynamic systems with fluctuating parameters*, Nauka, Moscow, 1975 (in Russian),

and system (3.49) is analysed in detail (by different methods) in Chapter 6 of this book. Apparently, these methods may be used in studying the behavior of models of even more complicated communities with their parameters displaying random fluctuations of the "white-noise" type.

More interesting results are to be obtained when considering the behavior of the generalized predator-prey system (with a non-linear trophic function) in random environments. For instance, in the work:

Sidorin A. P., Svirezhev Yu. M., "The dynamics of predator-prey system under conditions of random disturbances," *Dokl. Acad. Nauk SSSR*, Biological series, 4, pp. 573-579, 1980 (in Russian),

it is shown that a stable cycle in the predator-prey system may split into three cycles under random perturbations, two of which are stable and one is unstable.

CHAPTER 4

n-SPECIES COMMUNITIES

4.1. Ecological introduction

In quantitative analysis of a many species community the first obvious step, so common in ecology, to take on our road is the construction of the so-called *food* or *trophic webs*, i.e. graphs with vertices corresponding to species which constitute the community, and links indicating trophic interaction between species. Thus, for instance, Fig. 22 illustrates a part of a community trophic web, showing that out of 15 insect species (lower level) 5 species feed only on one of the two plant species, 2 more species feed only on the other one, while the diet of the rest 8 insect species comprises both plants.

Sometimes directed graphs are used for trophic webs: the direction of the link between two vertices indicates the one species which is the consumer of the other (i.e. the link direction coincides with the pathways of matter or biomass in the system).

In the community structure we can naturally distinguish the *trophic levels*—groups of species having no direct trophic interactions. There can be several levels: species of one level usually either compete for life resources or cooperate in resource utilization. Thus, the basic trophic levels of inland communities as a rule are made

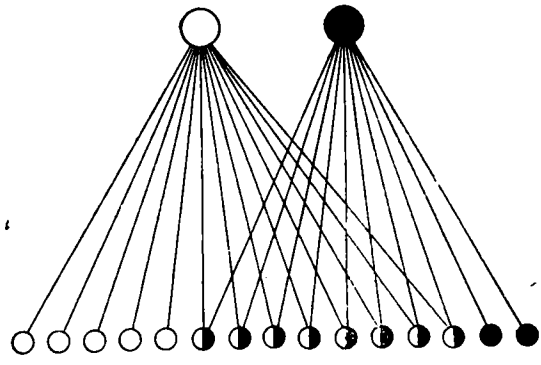

Fig. 22. An example of a trophic web. (From: E. Odum, *Fundamentals of ecology*, Saunders, Philadelphia, London, Toronto, 1971.)

of *producers* (plants which accumulate the energy of light and substrate), *primary consumers* (herbivorous) and *secondary consumers* (predators, preying on herbivorous) (Fig. 23). Sometimes the chain may be longer: for example, plants provide food for insects, insects are taken up by birds, which in turn serve as food to larger birds of prey.

If we consider not only the "who-eats-who" relations in the community structure, but take into account the transport of some nutrients and/or energy, then some feedback loops are revealed

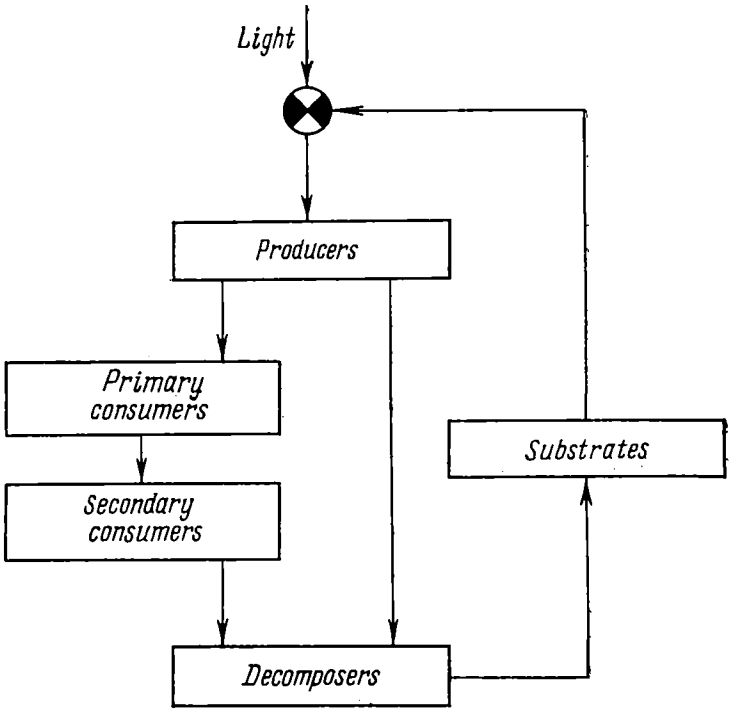

Fig. 23. Diagram of mass and energy flows between basic components of terrestrial ecosystems.

in the system: decomposers (microbes, bacteria, fungi, etc.) in the course of their vital activity split complex organic compounds (excrements, dead organic matter) into simpler mineral substances, used by producers (Fig. 23).

The presentation of community structure with trophic graphs, clearly, does not exhaust all the variety of interactions between species in the community. For one thing, these graphic structures only reflect pairwise interactions, while in natural systems the character of these interactions may be influenced not only by the environmental conditions but also by the presence of some other species. For another, the trophic web only shows the interactions between species of different trophic levels, i.e. interactions of the

predator-prey or host-parasite types, and gives no idea of pairwise interactions between species of one and the same level. In other words, the trophic web only presents the *vertical* structure of the community and gives no information about its *horizontal* structure. Meanwhile, species of one trophic level may demonstrate a variety of interrelationships.

The classification of all kinds of interspecific relationships is based on the idea, due to Odum, to classify the interactions between species not by their mechanisms on the specimen level—in this case the classification would turn boundless—but according to the effect produced by the interaction on the size of both interacting populations. Thus, for instance, if the population growth of one species suppresses the growth of the other, and the population growth of the second stimulates the growth of the first, the interaction is classed as the *predator-prey* (or host-parasite, or herbivorous-plants, etc.). If the population growth of both species has a positive effect on each of them, the interaction type is *mutualism* or *symbiosis*, and so on. The effect of one of the species on the other may be denoted by one of the signs: + (stimulating), — (suppressing), or 0 (neutral). Then the classification of pairwise interactions, obviously, consists of six main types:

+ + *mutualism*, or *symbiosis*;
+ — *predator-prey* (and the like);
+ 0 *commensalism*;
— — *competition*;
— 0 *amensalism*;
0 0 *indifference*.

If we enumerate all the n community species, the overall structure of pairwise interactions can be illustrated by the $n \times n$ sign-matrix of interactions S, each element (i, j) of which (+, — or 0) indicates the effect of the jth species upon the ith species. And the above-enumerated pairs of signs are composed by symmetric elements of matrix S. More details about the representation method for the overall structure of inter- and intraspecific relations in the community, as well as about the conclusions on the community stability that can be drawn out of only the known structure of interactions, are to be found in Sections 6 and 7.

Meanwhile all the foregoing leads us to only one obvious conclusion: a theoretical analysis of the n-species community dynamics in time is to be based upon a system of equations with respect to functions $N_i(t)$, approximating the species numbers, i.e. upon a model of the community studied. The solutions to the system, which are biologically sensible, belong to the positive orthant of the n-dimensional Euclidean space

$$P^n = \{N\colon N_1 \geqslant 0,\ N_2 \geqslant 0,\ \ldots,\ N_n \geqslant 0\},$$

and the community stability is interpreted as distinctive features of the special "equilibrium" solutions to the system.

In the class of ordinary differential equations the community model is a system of the form

$$\frac{dN_i}{dt} = F_i(N_1, \ldots, N_n; t), \tag{4.1}$$

where the set of functions $F_1, \ldots, F_n$ is defined by the structure of species interactions and their quantitative indices. If in equations (4.1) we characterize the natural birth and death-rates of species by linear terms and the self-limiting and counterplay between species—by quadratic ones, with no explicit relation to t, we arrive at the so-called Volterra models of n-species community dynamics. The present chapter, dealing with qualitative analysing method, is opened with the modern interpretation of Volterra's results for systems of this kind.

4.2. Volterra models and balance equations in ecology

In the recent literature on mathematical ecology the term *Volterra* models of n-species communities is commonly used for the systems

$$\frac{dN_i}{dt} = N_i\left(\varepsilon_i - \sum_{j=1}^{n} \gamma_{ij} N_j\right), \qquad i = 1, 2, \ldots, n, \tag{4.2}$$

where ε_i is the natural birth or death rate of ith species in the absence of all the other species, and the sign and absolute value of γ_{ij} $(i \neq j)$ refer respectively to the character and intensity of the influence of the jth species upon the ith species, γ_{ii} is the index of intraspecific interaction for the ith species. Matrix $\Gamma = \| \gamma_{ij} \|$, which reflects the structure of relations in the community, is often termed the *community matrix*; it is related to the sign-matrix S introduced in the preceding section by the relationship

$$S = -\text{sign}\, \Gamma.$$

Volterra derived system (4.2) proceeding from the following speculations: the ith species dynamics in the absence of all the others is given by the familiar logistic equation (generally, $\gamma_{ij} > 0$ indicating the intraspecific competition, or *self-limitation* in *size* of ith species), and the effect of the jth species upon the ith one is expressed by the term, proportional to the product $N_i N_j$ according to the so-called hypothesis of "encounters and equivalents". The hypothesis of "encounters and equivalents" states that variations of the ith species (prey) population due to preying of the jth species (predator) are determined by the number of encounters between individuals of the two species, hence the product $N_i N_j$;

and the predator population increases as if the eaten prey specimens were immediately transferred into predator specimens with a given proportionality coefficient—the "equivalent".

The hypothesis of "encounters and equivalents", that apparently owes its origin to the principle of "encounters" from statistical physics, can account for the form of equations (4.2) in the case of predator-prey interactions and, clearly, cannot justify it for other types of biological interactions. Moreover, its "non-biologicity" makes the hypothesis open to criticism on the part of ecologists. Nevertheless, it turns out that the Volterra equations (4.2) may be obtained using more natural assumptions.

Consider a community with a structure as illustrated in Fig. 23. Let us divide all the community components into three basic groups.

Producers with biomasses (or concentrations) x_i ($i = 1, 2, \ldots, m$). These are primarily green plants capable of fixing radiant energy and assimilating simple substances.

Consumers with concentrations y_j ($j = 1, 2, \ldots, n$). To this group we refer all the organisms, preying on other organisms, as well as decomposers which split the dead organics into simple substances taken up by the producers.

Substrates with concentrations c_k ($k = 1, 2, \ldots, p$). These are the abiotic substances (mainly the products of consumer vital activity), taken up by the producers.

Let us now set up mass-balance equations of each of these components. In essence, these equations are nothing but the mass conservation principles. These ecological balance equations can be written in the form

$$\frac{dx_i}{dt} = (F_x^i - D_x^i)\, x_i - \sum_{j=1}^{n} V_{ij} y_j + R_x, \qquad i = 1, \ldots, m, \tag{4.3}$$

$$\frac{dy_j}{dt} = (F_y^j - D_y^j)\, y_j - \sum_{r=1}^{n} v_{jr} y_r + R_y, \qquad j = 1, \ldots, n, \tag{4.4}$$

$$\frac{dc_k}{dt} = \sum_{j=1}^{n} U_{kj} y_j - \sum_{i=1}^{m} W_{ki} x_i + R_c, \qquad k = 1, \ldots, p, \tag{4.5}$$

where F^i and D^i are the natality and mortality functions for producers and consumers (with corresponding subscripts); V_{ij} is the preying function, giving the uptake rate of the ith producer-species biomass by the unit biomass of the jth consumer-species; v_{jr} is the preying function for the jth species uptake by the rth one (among consumers); W_{kj} is the function of the kth substrate uptake by the jth producer-species; U_{kj} is the intensity of kth substrate production by the jth consumer; R_x, R_y, and R_c, are the sums of inflows and

outflows of respective components. Naturally all these functions depend upon the environmental parameters (seasonal variations of humidity, temperature, etc.).

But such a model has one essential drawback—excessive generality. Proceeding from different biological speculations, the model functions should be made more concrete.

The natality of the ith species may be assumed to depend only upon the intensity of the radiation flux I and the amount of the uptaken substrates $\sum_{k=1}^{p} W_{ki}x_i$. From fairly natural considerations related to the conservation principles, we can assume that

$$F_x^i = \sum_{k=1}^{p} K_k^{(i)}(I)\, W_{ki}, \tag{4.6}$$

i.e. stoichiometrics takes place with coefficients $K_k^{(i)}$ which can be interpreted as the fraction of the kth substrate used for the reproduction of the ith producer biomass. Notice that if we consistently implement the stoichiometrics hypothesis, then

$$K_k^{(i)} = K_k, \qquad F_x^i = \sum_{k=1}^{p} K_k(I)\, W_{ki}. \tag{4.7}$$

For the growth rate of the jth consumer similarly to (4.6) we get

$$F_y^j = \sum_{i=1}^{m} K_i^{(j)} V_{ij} + \sum_{r=1}^{n} P_r^{(j)} v_{rj}, \tag{4.8}$$

where $K_i^{(j)}$ and $P_r^{(j)}$ are stoichiometric coefficients for consumers interacting with producers and for preying among consumers.

Consider one special case of the general model. Let the producers natality be limited neither in light nor in mineral nutrients, and be only restricted purely physiologically. Then F_x^i = const. Since the substrate-components in this case have no effect on the dynamics of other components, the model may only be reduced to producers-species and consumers-species. A similar situation arises when light is limiting, since light is an external factor with respect to this system, and when the radiation flux is constant, F_x^i may be considered constant as well. Examining the closed system we should set $R_x = R_y = R_c = 0$.

The most simple assumption as to the form of mortality functions is the hypothesis that they are constant. In natural communities the situation is more complicated: the intraspecific as well as interspecific competition for one and the same resource (food) makes the mortality to grow with increasing population of appropriate species. To describe this mechanism with balance relationships of some kind is hardly possible. Therefore the easiest assumption is a linear

relationship between the mortality functions and populations of species involved

$$D_x^i = m_x^i + \sum_{s=1}^{m} \mu_{is} x_s, \qquad D_y^j = m_y^j + \sum_{r=1}^{n} \nu_{jr} y_r, \tag{4.9}$$

where m_x^i and m_y^j are the coefficients of natural (physiological) mortality, μ_{ii} and ν_{jj} describe the intensity of intraspecific competition (if there is no competition for a common resource, μ and ν are to be zero).

What can be assumed about the form of the preying function? The easiest is the hypothesis of a linear relationship between these functions and the concentration (size, biomass) of the species preyed on

$$V_{ij} = \alpha_{ij} x_i, \qquad v_{jr} = \beta_{jr} y_j, \qquad r = 1, \ldots, n. \tag{4.10}$$

Of course, this assumption of a linear relationship between the preying functions and the diet holds in a very narrow range of concentrations of uptaken food (e.g. for low concentrations) and for a consumer's trophic strategy that makes no preference among species in the diet. But these assumptions, though restricted, do not contradict biology. Moreover, they are true of a very wide class of ecological situation. In the general case, clearly, there exist upper physiological boundaries to the amount of the food consumed (thus the preying functions should be given by relationships with saturations), as well as more complicated forms of trophic strategies (for example, the trophic preference results in a sequential instead of a simultaneous uptake of species; in this case the preying functions of a species have more complicated structures depending upon the concentrations of the other species as well).

Under the assumptions made above, the model (4.3)-(4.4) may be rewritten in the form

$$\frac{dz_k}{dt} = \varepsilon_k z_k - \frac{1}{b_k} \sum_{l=1}^{m+n} a_{kl} z_k z_l, \qquad k = 1, \ldots, m+n. \tag{4.11}$$

Here

$$z_k = \begin{cases} x_i, & k = i = 1, \ldots, m, \\ y_j, & k - m = j = 1, \ldots, n; \end{cases}$$

$$\varepsilon_k = \begin{cases} F_x^i - m_x^i, & k = i = 1, \ldots, m, \\ -m_y^j, & k - m = j = 1, \ldots, n; \end{cases}$$

$$\frac{1}{b_k} a_{kl} = \begin{cases} \mu_{is}, & k,\ l = i,\ s = 1,\ \ldots,\ m, \\ \alpha_{ij}, & k = i = 1,\ \ldots,\ m, \\ & l - m = j = 1,\ \ldots,\ n, \\ -K_i^{(j)}\alpha_{ij}, & k - m = j = 1,\ \ldots,\ n \\ & l = i = 1,\ \ldots,\ m, \\ \beta_{jr} - P_r^{(j)}\beta_{rj} + \nu_{jr}, & \\ & k - m,\ l - m = j,\ r = 1,\ \ldots,\ n. \end{cases}$$

System (4.11) (which can be written in the form (4.2) after a scaling substitution of variables $N_k = b_k z_k$ and the introduction of a matrix with elements $\gamma_{kl} = a_{kl}/(b_k b_l)$) represents the most general form of Volterra models. Volterra performed a detailed analysis for more particular cases—with some restrictions on the matrix $\| a_{kl} \|$. Considering the example of an "n predator-n prey" system we shall try to clear up the biological meaning of these restrictions. The system has the form

$$\frac{dz_k}{dt} = z_k \left(\varepsilon_k - \frac{1}{b} \sum_{l=1}^{2n} a_{kl} z_l \right), \qquad k = 1,\ \ldots,\ 2n; \tag{4.12}$$

$$a_{kl} = -a_{lk}, \qquad k \neq l; \qquad a_{kk} = 0.$$

Let all the predators be gathered on one trophic level, and all the prey on another, with no intra- or interspecific competition among species of one and the same level. Then if $z_1, \ldots, z_n$ are the prey populations, and $z_{n+1}, \ldots, z_{2n}$ are the predator populations, then

$$\frac{1}{b_k} a_{kl} = \begin{cases} 0, & k,\ l = 1,\ \ldots,\ n \quad \text{or} \quad k,\ l = n+1,\ \ldots,\ 2n, \\ \alpha_{kl}, & k = 1,\ \ldots,\ n \quad l = n+1,\ \ldots,\ 2n, \\ -K_l^{(k)}\alpha_{lk}, & k = n+1,\ \ldots,\ 2n, \quad l = 1,\ \ldots,\ n. \end{cases}$$

Hence a restriction on the form $a_{kl} = -a_{lk}$ will hold if and only if

$$K_l^{(k)} = K^{(k)}, \quad b_k = \begin{cases} 1, & k = 1,\ \ldots,\ n, \\ 1/K^{(k)}, & k = n+1,\ \ldots,\ 2n. \end{cases}$$

What can this condition imply? Turn again to the conservation principles. To this end, consider the case where m non-renewable substrates provide food for n species with biomasses y_j. From the conservation principles it follows that

$$\frac{dx_i}{dt} = \sum_{j=1}^{n} V_{ij} y_j, \qquad \frac{dy_j}{dt} = \sum_{i=1}^{m} K_i^{(j)} V_{ij} y_j, \tag{4.13}$$

and the total mass of substrates and the species uptaking them is to be constant, taking into account that only the fraction $K_i^{(j)}$

of the consumed ith substrate is used for the jth species reproduction. This holds if and only if $K_i^{(j)} = K_i$ for all j (strict stoichiometrics) and

$$\sum_{i=1}^{m} K_i x_i + \sum_{j=1}^{n} y_j = \text{const.} \tag{4.14}$$

This expression implies that only a fraction of each substrate mass goes into consumer biomass production (whatever the species). Everything is predetermined by the energetic and biochemical value of the uptaken substrate, and the specificity of species is characterized by the choice of the preying function.

There can be another approach. Let the balanced diet be determined by the preying functions, and the specificity of species be characterized be the fact that different species need different fractions of their diets ($K^{(j)}$) for their biomass reproduction. Then the conservation principle takes the form

$$\sum_{i=1}^{m} x_i + \sum_{j=1}^{n} y_j / K^{(j)} = \text{const.} \tag{4.15}$$

It is this case that is described by Volterra models. It is hard to judge which approach is more realistic. Apparently the truth lies somewhere in between. For us it is sufficient that the Volterra model is biologically sensible enough.

4.3. Stability in Volterra community models

Stability in (4.11)-type models is taken to mean existence and stability in Lyapunov's sense of the positive steady-state solution $\mathbf{N}^*$, i.e. the most stringent of all ecologically sensible requirements on the "equilibrium" trajectory of the community. The positive stationary solution to system (4.2) is to satisfy the linear algebraic system

$$\Gamma \mathbf{N}^* = \boldsymbol{\varepsilon} \tag{4.16}$$

where $\Gamma = \| \gamma_{ij} \|$, $\boldsymbol{\varepsilon} = [\varepsilon_1, \ldots, \varepsilon_n]$, n is the number of species. Let vector $\boldsymbol{\varepsilon}$ be such that all the entries of system (4.16) are positive, or in other words, $\mathbf{N}^*$ lies within the positive orthant P^n of the n-dimensional space. For instance, in system (4.12) this implies that at least $\varepsilon_i > 0$ for all the preys and $\varepsilon_j < 0$ for all the predators.

Examining systems (4.2), Volterra distinguished two large classes of such system—*conservative* and *dissipative*. System (4.2) is termed *conservative* if there exists a set of positive numbers $\alpha_1, \ldots, \alpha_n$

such that

$$F(N_1, \ldots, N_n) = \sum_{i,j=1}^{n} \alpha_i \gamma_{ij} N_i N_j \equiv 0; \tag{4.17}$$

if the quadratic form $F(N_1, \ldots, N_n)$ is positively definite, the system is called *dissipative.*

The biological implications of these definitions are as follows. If we identify the quantities α_i with the average values of specimen biomasses in each species, the expression

$$V(N_1, \ldots, N_n) = \alpha_1 N_1 + \ldots + \alpha_n N_n \tag{4.18}$$

gives the total community biomass. From equation (4.2), it follows immediately that the variation rate of total biomass is

$$\frac{dV}{dt} = \sum_{i=1}^{n} \alpha_i \varepsilon_i N_i - F(N_1, \ldots, N_n). \tag{4.19}$$

The first term on the right of (4.19) represents the effect of species growth and decline patterns (which are constant in this case), and the second term, the effect of species counterplay. Thus conservative communities are characterized by the fact that species interactions exert no influence on the total community biomass variations, while in dissipative systems these interactions slow down the total biomass growth.

Since in a conservative system the relations

$$\gamma_{ii} = 0, \qquad \alpha_i \gamma_{ij} + \alpha_j \gamma_{ji} = 0, \qquad i, j = 1, \ldots, n, \tag{4.20}$$

are obviously satisfied, i.e. γ_{ij} and γ_{ji} have different signs, it is clear that only those communities can be conservative, which have predator-prey relations as their only type of interspecific relations (excluding indifference), and lack species self-limiting. Volterra showed that the necessary and sufficient condition for system (4.2) to be conservative is provided by the following combination of requirements on the elements of matrix Γ:

(1) all $\gamma_{ii} = 0$,

(2) for $i \neq j$ either $\gamma_{ij} = \gamma_{ji} = 0$, or $\gamma_{ij}\gamma_{ji} < 0$;

(3) for an arbitrary sample of m different integers $p, q, r, \ldots, y, z$ from the set $\{1, 2, \ldots, n\}$ the relationship

$$\gamma_{pq}\gamma_{qr} \cdots \gamma_{yz}\gamma_{zp} = (-1)^m \gamma_{qp}\gamma_{rq} \cdots \gamma_{zy}\gamma_{pz}$$

is satisfied.

Thus, excluding the case $n = 2$, conservativity calls for the system parameters to satisfy some relationships of the equality type, thus making real-life systems unlikely to be conservative. Conservative communities in mathematical ecology is an idealization as systems without friction in mechanics, and just as in mechan-

ics we often neglect friction, so for some communities we can accept the approximate hypothesis of their being conservative.

The basic property of conservative systems (4.2) is the existence of the first integral along trajectories belonging to the positive orthant in the case of matrix Γ non-singularity (for even n):

$$\left(\frac{e^{N_1}}{N_1^{q_1}}\right)^{\alpha_1}\left(\frac{e^{N_2}}{N_2^{q_2}}\right)^{\alpha_2}\cdots\left(\frac{e^{N_n}}{N_n^{q_n}}\right)^{\alpha_n}=\text{const}, \tag{4.21}$$

where $\mathbf{q} = [q_1, \ldots, q_n]$ is the solution to system (4.16). At $\mathbf{q} = \mathbf{N}^* > 0$, on substituting the variables $n_i = N_i/N_i^*$ (4.21) may be reduced to

$$\left(\frac{e^{n_1}}{n_1}\right)^{\alpha_1 N_1^*}\left(\frac{e^{n_2}}{n_2}\right)^{\alpha_2 N_2^*}\cdots\left(\frac{e^{n_n}}{n_n}\right)^{\alpha_n N_n^*}=\text{const}. \tag{4.22}$$

Using these relationships, Volterra showed in particular, that when $\mathbf{q} > 0$ all the species are bounded from above and below by positive constants and, if the initial state of the system $\mathbf{N}(0)$ is distinct from $\mathbf{N}^*$, at least one species has undamped oscillations of population. In this case the *asymptotic means* for variables $N_i(t)$, i.e. the expressions

$$\frac{1}{t-t_0}\int_{t_0}^{t} N_i(\tau)\,d\tau$$

have limits as $t \to \infty$ which coincide with their steady state values (the principle of asymptotic means).

The trajectory behavior in a conservative system (4.2) can be looked at from the viewpoint of the first Lyapunov's method of the stability analysis of equilibrium $\mathbf{N}^*$. In fact, one can readily see, that the function

$$G(\mathbf{N}) = \sum_{i=1}^{n} \alpha_i (N_i - N_i^* \ln N_i) \tag{4.23}$$

is a Lyapunov function for the point $\mathbf{N}^*$ from the domain P^n: the minimal value of $G(\mathbf{N})$ is attained at the point $\mathbf{N}^*$ and the derivative along system trajectories $dG(\mathbf{N})/dt$ equals zero everywhere in P^n. Thus, the equilibrium $\mathbf{N}^*$ is Lyapunov stable (but not asymptotically).

The second Lyapunov method, based on system linearization at equilibrium point and the spectral analysis of the obtained matrix, gives insight into trajectory behavior in a small neighborhood of the equilibrium. Supposing

$$x_i = N_i - N_i^*,$$

we get a linear system

$$\frac{d\mathbf{x}}{dt} = -\operatorname{diag}\{N_1^*, \ldots, N_n^*\}\,\Gamma\mathbf{x}, \tag{4.24}$$

and if we consider deviations in the form

$$\nu_i = N_i/N_i^* - 1,$$

then

$$\frac{d\boldsymbol{\nu}}{dt} = -\Gamma \operatorname{diag}\{N_1^*, \ldots, N_n^*\}\,\boldsymbol{\nu}. \tag{4.25}$$

Since a linear substitution does not change the matrix spectrum in a linear system, matrices in (4.24) and (4.25) have a common spectrum. One can show that for $\mathbf{N}^* > 0$ this spectrum consists of pure imaginary numbers. In fact, if $\lambda = a + ib$ is an eigenvalue of matrix diag $\{\ldots\}\,\Gamma$ with the eigenvector $\mathbf{z} = u + iw$, then $\bar{\lambda} = a - ib$ is also an eigenvalue with the eigenvector $\bar{\mathbf{z}} = u - iw$. Then by definition of an eigenvector

$$(a + ib)\,z_k = \sum_{l=1}^{n} N_k^* \gamma_{kl} z_l,$$

$$(a - ib)\,\bar{z}_k = \sum_{l=1}^{n} N_k^* \gamma_{kl} \bar{z}_l, \qquad k = 1, 2, \ldots, n,$$

hence

$$(a + ib) \sum_k \alpha_k N_k^* z_k \bar{z}_k = \sum_k \sum_l \alpha_k \gamma_{kl} N_k^* N_l^* \bar{z}_k z_l,$$

$$(a - ib) \sum_k \alpha_k N_k^* \bar{z}_k z_k = \sum_k \sum_l \alpha_k \gamma_{kl} N_k^* N_l^* z_k \bar{z}_l.$$

Adding these equations term by term and rearranging the right hand-side, by (4.20) we get

$$2a \sum_k \alpha_k N_k^* \,|\, z_k \,|^2 = \sum_k \sum_l (\alpha_k \gamma_{kl} + \alpha_l \gamma_{lk})\, N_k^* N_l^* \bar{z}_k z_l = 0.$$

Hence, since $\alpha_k > 0$, $N_k^* > 0$ and not all of z_k are zero, it immediately follows that $a = 0$ what was required*.

Thus the linear approximation of trajectories in the equilibrium neighborhood is a superposition of $n/2$ sine curves with generally different periods. This is a typical example illustrating the potentialities of both Lyapunov's methods for a pure imaginary spectrum: direct linearization gives no definite answer as to whether or not N^* is stable or unstable, which can only be established by examination of an appropriate Lyapunov function.

* It should be noted that matrix Γ spectrum also consists of pure imaginary numbers, which provides one more necessary condition of system (4.2) being conservative.

If not all the components q_i of the solution for a steady-state system are positive, we can state that one or several species become extinct or their populations grow indefinitely. Otherwise, i.e. when all the populations are bounded from above and below by positive constants, there exist positive asymptotical means for all N_i^* which may be shown to be always equal to the appropriate roots q_i of system (4.16). The contradiction obtained proves the statement.

Thus the existence of a positive equilibrium manifests itself not only as a sufficient but also a necessary condition of stable operation of a conservative community.

Let us now turn to dissipative communities. From the dissipative system definition we obtain the necessary condition

$$\gamma_{ii} > 0, \qquad i = 1, 2, \ldots, n, \tag{4.26}$$

i.e. all species are to be self-limited. If we recall that in conservative systems all $\gamma_{ii} = 0$, it becomes clear that definitions for conservative and dissipative systems are incompatible. It is also clear that there may be systems which are neither conservative nor dissipative, say, systems in which only some species feature self-limitation.

The next necessary condition of dissipativity is that $\det \| \gamma_{ii} \| \neq \neq 0$, this suggesting the uniqueness of the solution to the system of steady-state equations. Finally, all the principal minors (i.e. those symmetric about the main diagonal) of matrix $\Gamma = \| \gamma_{ij} \|$ should be positive.

For a dissipative system (4.2) similarly to (4.21), Volterra derived the relationship

$$\prod_{r=1}^{n} \left\{ \frac{1}{n_r} \exp\left(\frac{|q_r|}{q_r} n_r \right) \right\}^{\alpha_r q_r} = C \exp\left\{ -\int_{t_0}^{t} F\left(\ldots, \left(1 - \frac{|q_r|}{q_r} n_r\right) q_r, \ldots \right) d\tau \right\}, \tag{4.27}$$

where $\mathbf{q} = [q_1, \ldots, q_n]$ is a solution to system (4.16) with no zero components, $n_r = N_r / |q_r|$, $C = \text{const} > 0$, and the quadratic form F is positive definite. If $\mathbf{q} = \mathbf{N}^* > \mathbf{0}$, the expression (4.27) is reduced to

$$\left(\frac{e^{n_1}}{n_1} \right)^{\alpha_1 N_1^*} \cdots \left(\frac{e^{n_n}}{n_n} \right)^{\alpha_n N_n^*} = C \exp\left\{ -\int_{t_0}^{t} F\left(\ldots, (1 - n_r) N_r^*, \ldots \right) d\tau \right\}. \tag{4.28}$$

Using this relationship Volterra proved that as $t \to \infty$ the state $\mathbf{N}^* > \mathbf{0}$ is limiting for all trajectories of the dissipative system (4.2) with positive initial values.

As with conservative systems, the study of trajectory behavior near $\mathbf{N}^*$ in the linear approximation is based on the evaluation of spectrum of matrix $-D\Gamma$ (or $-\Gamma D$), where $D = \operatorname{diag}\{N_n^*, \ldots, N_1^*\}$, and similarly to the above one can show that all the eigenvalues have negative real parts*. Thus the equilibrium $\mathbf{N}^*$ is locally asymptotically stable, and the way the perturbed trajectories approach $\mathbf{N}^*$ depends, as we know, upon the set of eigenvalues of $(-D\Gamma)$.

Note that for the function $G(\mathbf{N})$, introduced in (4.23), along the trajectories of system (4.2) we have the equality

$$G[\mathbf{N}(t)] = -\int_{t_0}^{t} F(\ldots, N_r(\tau) - N_r^*, \ldots)\, d\tau + \ln C - \sum_{r=1}^{n} \alpha_r N_r^* \ln N_r^*.$$

Hence

$$\frac{dG}{dt} = -F(\ldots, N_r(t) - N_r^*, \ldots) \leqslant 0$$

everywhere in the domain P^n, and $dG/dt = 0$ only when $\mathbf{N}(t) = \mathbf{N}^*$. This implies that $G(\mathbf{N})$ is a Lyapunov function for the equilibrium $\mathbf{N}^*$ in the domain P^n. Therefore, $\mathbf{N}^*$ is globally asymptotically stable within the positive orthant, thus explaining the general character of trajectories behavior in the dissipative system, described by Volterra based on other considerations.

As to the case where not all the q_r are positive, if there is only one negative root, the corresponding species disappears**; if there are several such roots, among the species involved at least one is to disappear. Thus, both for dissipative, and for conservative systems the existence of a stable equilibrium $\mathbf{N}^* > 0$ proves to be not only a sufficient, but also a necessary condition of stable operation of the community.

4.4. Predator-prey patterns

As mentioned in the previous section, only those communities may be conservative, which comprise predator-prey species with no self-limitation. From conditions (4.20) it follows that symmetric entries of matrix Γ should have opposite signs; in particular, Γ may be anti-symmetric. For a conservative system to be stable it is necessary and sufficient for the system of steady-state equations (4.16) with a non-singular matrix Γ to have a positive solution. Evidently, this can be always attained by the choice of suitable ε_i values; for instance, it is sufficient to assume $\varepsilon = \Gamma\,[1, 1, \ldots, 1]^T$. Thus, stability of a conservative community is reduced just to the existence

* The same is true of matrix Γ, which gives another necessary condition of dissipativity of system (4.2).

** That is $\lim\limits_{t\to\infty} N_r(t) = \lim\limits_{t\to\infty} [\inf\limits_{\tau\leqslant t} N_r(\tau)] = 0$.

of a positive solution for (4.16), or to the non-singularity of the community matrix Γ, if the problem statement allows ε to vary. It turns out that stability may be assessed through analysis of the community trophic graph alone. The results of the present section indicate that the predator-prey community (with no self-limitation) is stable only if the species pool can be so divided into disjoint pairs, that in each pair one of the species is preying on the other.

Every real $n \times n$-matrix $A = \| a_{ij} \|$ can be related to a directed graph with n vertices, such that vertices i ang j are connected by

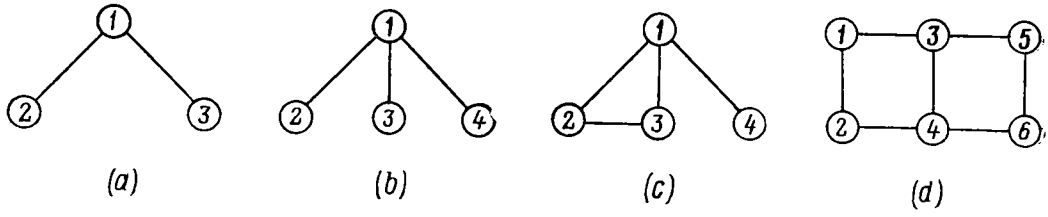

Fig. 24. Graphs of predator-prey communities.

a link $j \to i$ if and only if $a_{ij} \neq 0$. For a conservative community matrix Γ, obviously, if there is a link $j \to i$, there also exists a contrariwise directed link, and therefore such a community structure may be presented by a non-directed graph. We denote this graph by $G(\Gamma)$.

A subset P of the set of all links $G(\Gamma)$ is said to give a *predator-prey pairing*, if there is not a single vertex among those belonging to links from P, that is a vertex of more than one link. The predator-prey pairing will be termed *complete predator-prey pairing*, if it comprises all the n vertices of the graph. The graphs shown in Fig. 24*a*, *b* have no complete pairings; the latter features a complete pairing when the link 2-3 is added (Fig. 24*c*); for the graph of Fig. 24*d* a complete pairing may be carried out in three different ways.

Theorem 1. Let A be an anti-symmetric matrix, and $G(A)$ be a graph (non-directed) associated with A. Then if A is non-singular, $G(A)$ features a complete predator-prey pairing. Conversely, if $G(A)$ has a complete predator-prey pairing, there exists a non-singular anti-symmetric matrix B such that

$$G(B) = G(A),$$

and the B entries may be chosen arbitrarily close to the corresponding A entries.

This theorem, which is proved below, indicates, that the existence of a complete pairing is a necessary condition of stability for a community with an anti-symmetric matrix A. This condition is also sufficient in the sense that if A is singular, then a matrix B is arbit-

rarily close to A already non-singular and presents a stable community. Theorem 1 makes it possible to say at once that the community with a graph of Fig. 24*a* is unstable (as was already noted by Volterra, such systems can be stable only for even n); the system in Fig. 24*b* is unstable as well.

In the structure of many real predator-prey communities, generally, we can distinguish *trophic levels*, i.e., aggregates of species, which feed only on species in the next level and provide food to species in the previous one. The graph in Fig. 25 gives an example of a community where species *1* preys on species *2*, *3*, and *4*, to which food is provided by species *5* and *6*, and so on. If the trophic levels in a graph do not show up, the following definition may be of use.

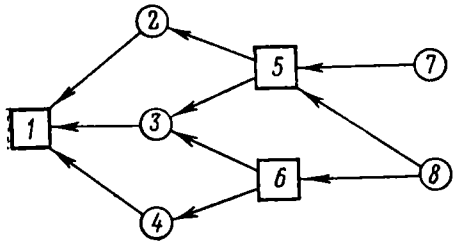

Fig. 25. A graph with trophic levels. Arrows form the prey to the predator.

Graph $G(A)$ will be called *trophic*, if there exists a subset T of species such that none of them feed on species from T, whereas species not in T feed only on species in T. For multilevel systems this formal definition evidently holds, since for T we can take the union of levels which are at an odd "distance" from prey at the last level (in Fig. 25 vertices of T are denoted by squares).

Theorem 2. If A is a non-singular matrix and graph $G(A)$ is trophic, then $G(A)$ features a complete predator-prey pairing.

From Theorem 2 we directly obtain the necessary conditions, facilitating the hunt for a complete pairing in graphs with several trophic levels. Let the graph G belong to a non-singular matrix with trophic levels $i = 1, 2, \ldots, l$; λ_i be the number of species in the ith trophic level. From Theorem 2 it follows that:

If $l = 2$, then $\lambda_1 = \lambda_2$ (or else there will be no complete pairing).

If $l = 3$, then $\lambda_1 + \lambda_3 = \lambda_2$ (obviously $\lambda_1 < \lambda_2$ and $(\lambda_2 - \lambda_1)$ species in the 2nd level should be connected with λ_3 species in the 3rd level in the pairing).

If $l > 3$, then $\lambda_i = \alpha_i + \beta_i$ $(i = 1, \ldots, l)$, where $\alpha_i \geqslant 0$, $\beta_i \geqslant 0$, $\alpha_1 = \beta_l = 0$, $\beta_i = \alpha_{i+1}$.

The last condition is not met for the graph in Fig. 23, therefore it has no complete pairing, and hence the corresponding anti-symmetric matrix is singular.

We direct our attention now to the proof of the theorems formulated above. Let A be an anti-symmetric matrix, and the complete pairing $G(A)$ be given by a subset P of links. We define matrix $B(z)$ in the following way:

$$b_{ij} = \begin{cases} a_{ij}, & \text{if the link corresponding to } a_{ij} \text{ is in } P, \\ za_{ij} & \text{otherwise.} \end{cases}$$

Then

$$\det B(z) = \pm \prod a_{ij}a_{ji} + p(z), \tag{4.29}$$

where the product is taken over all pairs of A elements, which correspond to links from P, and the polynomial $p(z)$ is such that $p(0) = 0$. Then $\det B(0) \neq 0$ and in general $\det B(z) \neq 0$, except for a finite set (not more than n) of values z. Suppose that z_0 is close enough to 1 (but not equal to 1, if $\det B(1) \neq 0$). Then the matrix sought is

$$B = B(z_0)$$

and the second part of Theorem 1 is proved.

Notice that the proof does not require A to be anti-symmetric and relies only on the property that

$$\text{sign } a_{ij} = -\text{sign } a_{ji} \tag{4.30}$$

Let now $\det A \neq 0$. By the standard rule we relate matrix A to a directed graph $G'(A)$. In the expansion

$$\det A = \sum_{\sigma} \text{sign } \sigma a_{1\sigma(1)} \ldots a_{n\sigma(n)} \tag{4.31}$$

a permutation σ of numbers from 1 to n can be found, such that the corresponding term of the determinant

$$a_{1\sigma(1)} \ldots a_{n\sigma(n)}$$

is different from zero. This permutation is related to a subgraph G''_σ of graph G', comprising all the n vertices, each of which being the head of exactly one link and the tail of exactly one link in G''_σ. Then by Euler theorem* G''_σ is a disjoint union of directed cycles. Notice that for every link in G''_σ according to (4.30) we can find a contrariwise directed link in G', and hence a non-directed link between the same vertices in $G(A)$. Now if all the cycles G''_σ have even lengths, the complete predator-prey pairing of $G(A)$ is given by the set P of those links, which relate to links in G''_σ.

If graph $G(A)$ is trophic, all cycles G''_σ are to be of even length (each cycle being a number of jumps from the set of vertices T into $\overline{T}$ and backwards), thus proving theorem 2.

Suppose now that for every permutation σ, presented by a non-zero term in the expansion (4.31), a cycle of odd length may be found in G''_σ. According to (4.30) all non-zero terms can be grouped together into classes according as whether or not they yield the same G''_σ, allowing either orientation of each cycle. Each such class C then defines a non-directed graph G'' with cycles along the same

* Berge, C. *The Theory of Graphs and its Applications.* Wiley, New York, Chap. 17, 1962.

vertices as those in G''_σ, whereas summing up the terms in (4.31) through this class gives the determinant of some anti-symmetric matrix A^C with elements

$$a_{ij}^C = \begin{cases} a_{ij}, & \text{if } a_{ij} \in G'', \\ 0, & \text{otherwise.} \end{cases}$$

Properly reordering the species we obtain A^C in a block-diagonal form with blocks belonging to cycles G''. By the assumption, among them there are cycles of odd length and, since an anti-symmetric determinant of an odd order equals zero, the determinant of A^C, given by the product of block determinants, also equals zero. Therefore

$$\det A = \sum_C \det A^C = 0,$$

and the contradiction obtained concludes the proof of Theorem 1.

A large number of species in the predator-prey community structure can make the search for a complete pairing rather difficult. The problem is alleviated by specific algorithms, enabling us to establish a pairing comprising the maximal number of graph vertices, and hence the complete pairing, if any.

4.5. Dissipativity and stability of community matrix

What can we say about stability in Volterra systems of general form (4.2)? If the quadratic form given by the community matrix Γ is not somehow restricted *a priori*, meaningful information about the stability of equilibrium $\mathbf{N}^*$ may only be obtained by linearizing the appropriate matrix and studying its spectrum. For local asymptotic stability of $\mathbf{N}^*$ it is sufficient for matrix $D(-\Gamma)$, where $D = \operatorname{diag}\{N_1^*, \ldots, N_n^*\}$, to be stable, i.e. for all its spectrum in the complex plane to lie on the left of the imaginary axis. Notice that the elements of this matrix depend both upon the structure of interactions (matrix $\Gamma = \| \gamma_{ij} \|$) and upon the equilibrium values N_i^*, which for a given Γ are defined by the variables ε_i, i.e. characteristics of separate species not involved in interaction. Equilibrium stability thus appears as a property of both species relations in the community, and separate species characteristics. What can be said about matrix Γ, if the stability is required to be determined only by the combination of interspecific relations independent of the indices of species intrinsic natural growth or decline? In other words, what should the matrix Γ be for $\mathbf{N}^*$ stability to be only determined by properties of Γ and be preserved for all admissible ε_i values?

Since a suitable choice of ε_i can always give arbitrary preassigned N_i^* values (system $\Gamma^{-1}\boldsymbol{\varepsilon} = \mathbf{N}^*$ can be uniquely solved for $\boldsymbol{\varepsilon}$), the requirement stated above implies that matrix $D(-\Gamma)$ is to be stable

for all values $N_i^* > 0$, or, in other words, matrix $-\Gamma$ is to remain stable when premultiplied by an arbitrary positive diagonal matrix D. This matrix property in mathematical economics has been called *D-stability*.

That the notion of D-stability has sense, is supported by the fact that there may be stable matrices with no D-stability*. The following conditions for D-stability are known.

Necessary condition. If A is D-stable, then no principal odd-order minor of A is positive and no principle even-order minor of A is negative, and at least one non-zero principal minor of A of every order exists.

Sufficient condition. If there exists a positive diagonal matrix B such that $BA + A^TB$ is negatively definite, then A is D-stable**.

For instance, a symmetric negative definite matrix A is D-stable, since matrix $I/2$ can be used for B in this case. Moreover, matrix $-\Gamma$ of any dissipative system (4.2) is D-stable. In fact, by the definition of dissipativity, there exists a matrix $\mathfrak{A} = \operatorname{diag}\{\alpha_1, \ldots, \alpha_n\}$ with positive α_i, such that the quadratic form $F(\mathbf{x}) = (\mathfrak{A}\Gamma\mathbf{x}, \mathbf{x})$ is positive definite***. And this, in turn, is equivalent to matrix (symmetric)

$$\frac{1}{2}[\mathfrak{A}\Gamma + (\mathfrak{A}\Gamma)^T] = \frac{1}{2}\mathfrak{A}\Gamma + \Gamma^T\frac{1}{2}\mathfrak{A}$$

being positive definite, whence it follows that $\mathfrak{A}/2$ can be taken as B for matrix $-\Gamma$, therefore the sufficient D-stability condition holds for $-\Gamma$.

The class of D-stable matrices is by no means exhausted by dissipative systems. This immediately follows from the example of a 2×2 matrix $-\Gamma$ with the sign pattern

$$S = \begin{Vmatrix} - & + \\ - & 0 \end{Vmatrix},$$

which is D-stable but cannot be dissipative as it has a zero entry on the main diagonal [cf. condition (4.26)]. D-stability leads to a yet stronger property of matrices: matrix A is said to be *totally stable* if every principal submatrix of A is D-stable. This definition immediately suggests that every principal submatrix of a totally stable matrix is also totally stable. In consequence, total stability may be naturally interpreted for communities: a community, remain-

* For instance, since the necessary condition for the 2×2 matrix $A = \| Q_{ij} \|$ to be stable is the inequality $a_{11} + a_{22} < 0$, clearly, when a_{11} and a_{22} are of different signs, there exist matrices D such that DA loses stability.

** This condition is similar in form to the well-known Lyapunov criterion of stability of matrix A which uses some positive definite matrix instead of B.

*** In this case the non-symmetric matrix $\mathfrak{A}\Gamma$ is named *positive quasidefinite*.

ing after any combination of species has been excluded from the interactions pattern, still preserves total stability.

A *necessary* condition for matrix A to be totally stable is that every principal even-order minor of A is positive and every principal odd-order minor of A is negative. The condition results from the fact that principal minors are determinants for stable principal submatrices.

It is interesting to make clear how the properties of total stability of matrix $-\Gamma$ and the dissipativity of system (4.2) with matrix Γ are related to each other. Notice that, though the definitions of Section 3 have been given for systems of equations, the conservativity and dissipativity properties are actually properties of the corresponding matrices Γ and may be reformulated directly for matrices. Thus matrix A will be termed *dissipative*, if there exists a positive diagonal matrix $\mathfrak{A}$ such that $-\mathfrak{A}A$ is positive quasidefinite, that is, the form $(-\mathfrak{A}A\mathbf{x}, \mathbf{x})$ is positive definite, or $(\mathfrak{A}A\mathbf{x}, \mathbf{x})$ is negative definite; *conservativity* of matrices is evidently defined too*.

Before investigating the relationship between dissipativity and total stability, let us show that if a matrix A is stable, or D-stable, or dissipative, then matrices A^T and A^{-1} respectively have the same property.

In fact, A and A^T spectra coincide, whereas A^{-1} eigenvalues equal $1/\lambda$, where λ is an A eigenvalue. Further, if for any D matrix DA is stable, then both matrix AD, similar to the latter and the transpose of the latter $(AD)^T = DA^T$ are stable, that is, matrix A^T is D-stable. In this case matrix $(DA)^{-1} = A^{-1}D^{-1}$ is also stable, whence D-stability for A^{-1} follows. Lastly, if A is dissipative, a diagonal matrix $\mathfrak{A}$ may be found such that the form

$$(A\mathfrak{A}\mathbf{x}, \mathbf{x}) = (\mathbf{x}, \mathfrak{A}A^T\mathbf{x}) = (\mathfrak{A}A^T\mathbf{x}, \mathbf{x})$$

is negative definite, giving matrix A^T dissipativity. Since A^T is dissipative, there is a matrix $\mathfrak{A}$ such that

$$(\mathfrak{A}A^{-1}\mathbf{x}, \mathbf{x}) = (A^{-T}A^T\mathfrak{A}A^{-1}\mathbf{x}, \mathbf{x}) = [A^T\mathfrak{A}(A^{-1}\mathbf{x}), A^{-1}\mathbf{x}]$$

is negative definite, whence A^{-1} dissipativity follows.

If in a quadratic form of fixed sign we equate some variables to zero, the form will still have a fixed sign with respect to the remaining variables. Thus, any principal submatrix A' of a dissipative matrix A is itself dissipative and, thus, D-stable. It follows that any dissipative matrix is totally stable.

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* In equivalent terms multiplication by a diagonal matrix from the right is considered: the form $(-A\mathfrak{A}\mathbf{x}, \mathbf{x})$ is either positive definite or identically zero.

From all the above speculations the following picture appears for stability of matrix A

$$\boxed{\text{Dissipativity}} \Rightarrow \boxed{\text{Total stability}} \Rightarrow \boxed{D\text{-stability}} \Rightarrow \boxed{\text{Stability}} \tag{4.32}$$

Returning to the community matrix $-\Gamma$ for the Volterra system (4.2), one can see that the first three properties in diagram (4.32) are sufficient for the equilibrium $\mathbf{N}^* > 0$ to be stable (asymptotically, according to Lyapunov), while from the stability of $-\Gamma$ alone no such conclusion can be drawn: for some N_i^* values the equilibrium may be stable, for others not.

There exists, however a whole class of matrices for which all the properties in diagram (4.32) are equivalent. These are the so-called *normal* matrices, i.e. matrices with the property that $AA^* = A^*A$ (in the real case $AA^T = A^TA$). For example, symmetric and antisymmetric matrices are normal, or in terms of communities, these are competition matrices with the same interspecific influence, and community matrices built up only of predator-prey kinds without self-limitation and equal absolute values of γ_{ij} and γ_{ji}.

A real normal matrix can be made diagonal by a unitary similarity transformation:

$$A = U^* \operatorname{diag}\{\lambda_1, \ldots, \lambda_n\} U, \tag{4.33}$$

where $U^* = U^{-1}$ and $\lambda_1, \ldots, \lambda_n$ are the eigenvalues of A. Then

$$A^T = A^* = U^* \operatorname{diag}\{\bar{\lambda}_1, \ldots, \bar{\lambda}_n\} U,$$

$$\frac{1}{2}(A + A^T) = U^* \operatorname{diag}\{\operatorname{Re}\lambda_1, \ldots, \operatorname{Re}\lambda_n\} U,$$

i.e. the real parts of a normal matrix eigenvalues are equal to the eigenvalues of a symmetric matrix $\frac{1}{2}(A + A^T)$:

$$\operatorname{Re}\lambda(A) = \lambda\left[\frac{1}{2}(A + A^T)\right]. \tag{4.34}$$

If a normal matrix A is stable, then $\operatorname{Re}\lambda(A) < 0$ and the matrix $A + A^T$ is negative definite. Therefore A is dissipative, thus suggesting the equivalence of all stability definitions in diagram (4.32) for normal matrices.

4.6. Qualitative stability

In the preceding section we looked at the notion of D-stability of community matrices, which for Volterra models implies invariant equilibrium stability with respect to any variations in coefficients of natural growth and decline of ε_i if only $\mathbf{N}^* > 0$ exists for them.

Equilibrium stability is thus defined solely by the combination of intra- and interspecific relationships in the community. An even stronger from the mathematical and no less interesting from the ecological viewpoint is the case where stability is sustained for any magnitudes of entries in matrix $\Gamma = \| \gamma_{ij} \|$ provided only that the *type of* pairwise *interaction* between species is preserved. Such a community property is called *qualitative stability*. In other words, qualitative stability indicates that the community remains stable at any intensities of the existing intra- and interspecific interactions.

Suppose the dynamics of an n-species community is given by a system of equations of the general form

$$\frac{dN_i}{dt} = f_i(\mathbf{N}), \qquad i = 1, 2, \ldots, n \tag{4.35}$$

with the functions f_i (N) which allow the existence of an equilibrium $\mathbf{N}^* > 0$ and may be linearized at this point. Then the linearized matrix of system (4.35) at the point $\mathbf{N}^*$

$$A = \left\| \frac{\partial f_i(\mathbf{N})}{\partial N_i} \bigg|_{\mathbf{N}^*} \right\| \tag{4.36}$$

gives the structure of species interactions in the community. This matrix is known as the *community matrix*. Each its element $a_{ij} = \partial f_i / \partial N_j$ indicates the character (sign) and the intensity (absolute value) of jth species effect upon the ith species, thus the sign matrix introduced in Section 1 and presenting the pattern of species interactions is nothing but

$$S = \operatorname{sign} A = \left\| \operatorname{sign} \frac{\partial f_i(\mathbf{N})}{\partial N_j} \bigg|_{\mathbf{N}^*} \right\|. \tag{4.37}$$

The fact that system (4.35) may have several steady states instead of one, with generally different matrices S, does not contradict biology, since in nature systems are known with patterns of species interactions varying with the system state.

Qualitative stability is obviously a property of only the sign pattern S of a community matrix A and according to (4.37) may be formulated in matrix terms: matrix A is called *qualitatively stable* (or *sign-stable*), if it remains stable at any absolute values of its non-zero elements. In other words, A remains stable for all numerical variations of its elements, which do not violate the sign pattern $S = \operatorname{sign} A$.

If A has no sign stability, then in the framework of a given sign pattern there are values a_{ij} such that the spectrum of A includes eigenvalues with $\operatorname{Re} \lambda_i \geqslant 0$; it is also possible that sets $\{a_{ij}\}$ exist for which A is still stable. That is, for some magnitudes of the interactions between species the community may be stable, whereas for others unstable.

Qualitative stability of system (4.35) is in a sense (within the domain of linearization method) an equivalent of its structural stability, i.e. the property to keep $\mathbf{N}^*$ stable for all permissible variations in parameters of functions f_i (N). The set of permissible variations are those parameter values which preserve the sign pattern S and allow the existence of the equilibrium $\mathbf{N}^* > 0$.

It should be noted that the trophic community graphs characterized in Section 1 cannot determine a unique community sign pattern without additional concrete information about interactions between species in one and the same trophic level, i.e. there is no one-to-one correspondence between trophic graphs and matrices S. This correspondence is attained, when graph vertices are connected by directed links with signs + or — attached by the following rule: if species j effects somehow species i, the link $j \to i$ is drawn and the sign of the effect is attached to it (Fig. 26). This construction is called a *signed directed graph*, and in what follows will be abbreviated as SDG. Qualitative stability of a community is obviously a property of its SDG, and the conditions of qualitative stability may be formulated both in matrix terms and in terms of the associated SDG.

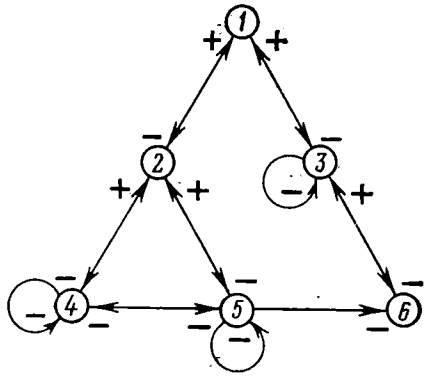

Fig. 26. Signed directed graph of the community. Species *1* preys on *2* and *3*, which in turn prey on species *4*, *5*, *6*; *4* and *5* are linked by competition, relations of amensalism are between species *6* and *5*; species *3*, *4*, *5* regulate their own populations.

There is a variety of necessary and sufficient conditions for matrix sign stability, and the necessity of the conditions is most usually proved by using the determinant criterion of Routh-Hurwitz, while sufficiency is established by Lyapunov criterion of matrix stability.

Until recently the following combination of conditions, obtained by J. Quirk and R. Ruppert when studying matrices in models of mathematical economics, was considered the sign stability criterion for a real indecomposable $n \times n$ matrix $A = \| a_{ij} \|$:

(1) $a_{ij}a_{ji} \leqslant 0$ for all $i \neq j$,

(2) for any sequence of 3 or more indices $i_1 \neq i_2 \neq \ldots \neq i_m$ the inequalities $a_{i_1 i_2} \neq 0$, $a_{i_2 i_3} \neq 0, \ldots, a_{i_{m-1} i_m} \neq 0$ imply $a_{i_m i_1} = 0$;

(3) $a_{ii} \leqslant 0$ for all i, $a_{i_0 i_0} < 0$ for some i_0;

(4) there exists a non-zero term in the expansion of det A.

Conditions (1) and (3) are easily restated in ecological terms (1) requires that no competitive or symbiotic relations be presen: in the community; (3) implies that no species exhibit a positive feedback and at least one species has a self-stabilizing effect. Condi-

tion (2) forbids directed cycles of three or more members in the community SDG.

Formally condition (4) demands that there exist a permutation τ of indices 1, 2, . . ., n such that

$$s_{1,\sigma(1)}\, s_{2,\sigma(2)} \quad \ldots \; s_{n,\sigma(n)} \neq 0, \tag{4.38}$$

where s_{ij} are the elements of the sign matrix $S = \operatorname{sign} A$. Any permutation σ may be represented as a cyclic structure

$$\sigma = c_1 \ldots c_p$$

with cycles c_j with l_j members such that

$$1 \leqslant l_j \leqslant n, \qquad \sum_{j=1}^{p} l_j = n.$$

A group of non-zero factors from (4.38)

$$a_{i_1 i_2} \neq 0, \qquad a_{i_2 i_3} \neq 0, \; \ldots, \qquad a_{i_{l-1} i_l} \neq 0, \qquad a_{i_l i_1} \neq 0.$$

belongs to every cycle $c = (i_1, i_2, \ldots, i_l)$ with l members. This corresponds to a directed loop in the SDG drawn through vertices $i_1, \ldots, i_l$. Thus, condition (4) implies that there exists at least one SDG subdivision into disjoint cycles with the total number of members n. Since condition (2) forbids cycles of three and more members, taking (1) into account gives that in a SDG of a qualitatively stable community k pairs $(0 \leqslant k \leqslant n/2)$ of predator-prey species may be distinguished such that the remaining $n-2k$ species exhibit self-stabilizing effects (presenting 1-cycles).

That the matrix is *indecomposable* is a very essential point in stating conditions (1)-(4). Recall that matrix A is termed *decomposable*, if a permutation of its rows and corresponding columns can rearrange it to the form

$$A = \begin{Vmatrix} B & 0 \\ C & D \end{Vmatrix} \tag{4.39}$$

where B is a $p \times p$ matrix and D is a $q \times q$ matrix $(p + q = n)$. For a community, indecomposable means that no group of p species $(1 \leqslant p \leqslant n)$ can be found such that the other n-p species be unaffected by it. Or in the graph, no p vertices can be chosen such that not a single arrow from the other n-p vertices points at them.

The necessary condition of indecomposability is that there is at least one non-zero diagonal element in every row and every column of the matrix. In fact, if, say, the ith row fails to satisfy this condition, then a permutation of indices, transforming i into 1, and vice versa, produces a matrix with $a_{12} = a_{13} = \ldots, = a_{1n} = 0$, that is, decomposability takes place.

The indecomposability condition may be ecologically interpreted as follows: each species in the community is necessarily affected by at least one of the other species and is, in turn, influencing at least one of the other species. The graph in Fig. 26 belongs to an indecomposable matrix, however it fails to satisfy conditions (1) and (2). Meanwhile, a decomposable matrix

$$\begin{Vmatrix} -a & b & c \\ 0 & 0 & -d \\ 0 & e & 0 \end{Vmatrix}, \qquad a,\ b,\ c,\ d,\ e > 0, \tag{4.40}$$

(SDG in Fig. 27) satisfies conditions (1)-(4), but has a pair of purely imaginary numbers $\lambda_{1,2} = \pm i\sqrt{de}$ ($\lambda_3 = -a$) in its spectrum, therefore it is not even stable.

It turns out that the indecomposability of matrix A restricts even more the diversity of interspecific relations in qualitatively stable community. This results from the following Lemma, which deals with the notion of "symmetric" and "asymmetric" pattern of zeros. A matrix is said to be of *symmetric pattern* if $a_{ij} \neq 0$ implies $a_{ji} \neq 0$ for any $i \neq j$ while a matrix is of *asymmetric pattern* if for some $i \neq j$ $a_{ij} = 0$ and $a_{ji} \neq 0$.

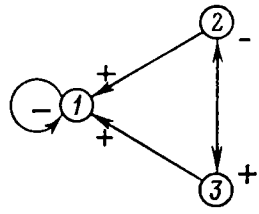

Fig. 27. Self-regulating special-commensal *1* is related to the *3-2* pair predator-prey.

Lemma 1. If A satisfies condition (2) and is of asymmetric pattern, A is decomposable.

Proof. For an asymmetric pattern A there exists an element $a_{ij} \neq 0$ ($i \neq j$) such that $a_{ji} = 0$. Reindexing A with the permutation of indices

$$\begin{pmatrix} 1 & 2 \ldots i \ldots j \ldots n \\ i & j \ldots 1 \ldots 2 \ldots n \end{pmatrix},$$

we get $a_{12} \neq 0$, $a_{21} = 0$. If now A has no non-zero elements to the right of a_{22}, the matrix is decomposable. Otherwise, if there are non-zero elements to the right of a_{22}, let $a_{2j} \neq 0$ be the first of them. Reindexing $3 \rightleftarrows j$ then yields $a_{23} \neq 0$ whence by condition (2) $a_{31} = 0$, i.e. A becomes

$$A = \begin{Vmatrix} * & \varnothing & * & * & \ldots \\ 0 & * & \varnothing & * & \ldots \\ 0 & * & \ldots & & \\ * & \ldots & & & \\ \ldots & & & & \end{Vmatrix},$$

where the asterisk is an arbitrary and $\varnothing$ a non-zero element.

If the procedure can be repeated for the 3rd, 4th, . . ., nth row,

i.e., if each of them has non-zero elements to the right of the diagonal, then the first column of A, with all the elements below a_{11}, consists solely of zeros, thus implying that A is decomposable. Otherwise, assume that the first row without non-zero elements to the right of the diagonal is the mth, i.e. $a_{m,m+1} = a_{m,m+2} = \ldots = a_{mn} = 0$ and

$$A = \left\| \begin{array}{cccccccc|c} * & \emptyset & * & \ldots & & & * & \ldots & 1 \\ 0 & * & \emptyset & * & & \ldots & * & \ldots & 2 \\ \vdots & & \ddots & & & & & A^\circ & \\ 0 & * & \ldots & & * & \emptyset & * & \ldots & m-1 \\ 0 & * & \ldots & & & * & 0 & 0\ldots 0 & m \\ * & \ldots & & & & & & & \\ \ldots & & & & & & & & \end{array} \right\|$$

If now the submatrix $A^\circ = A\begin{pmatrix} 2, & 3, & \ldots, & m-1 \\ m+1, & \ldots, & & n \end{pmatrix}$ consists only of zeros, reindexing $1 \rightleftarrows m$ we get a non-zero $(m-1) \times (n-m+1)$ block in the upper right corner of A, therefore, A is again decomposable. If there is an $a_{ij} \neq 0$ in submatrix A°, reindexing $j \rightleftarrows m+1$ we do not affect the first m rows and columns and get $a_{i,\,m+1} \neq 0$ $(2 \leqslant i \leqslant m-1)$. Since $a_{12} \neq 0$, $a_{23} \neq 0$, $\ldots$, $a_{i-1,i} \neq 0$, it follows from condition (2) that $a_{m+1,1} = 0$. Consider further the $(m+1)$th row: either there are non-zero elements to the right of the diagonal and then $a_{m+2,1} = 0$, or all of these elements are zeros and then we turn to submatrix A°. If it still has non-zero elements, reindex, as before, one of them into the $(m+2)$th column and by condition (2) we get $a_{m+2,1} = 0$. Eventually thus we either exhaust all non-zero elements in A° and obtain a block of zeros in the upper right corner, or find $a_{n1} = 0$ in the first column, both resulting in decomposability of A. This proves Lemma 1.

From Lemma 1 and condition (1) it immediately follows that symmetric non-zero elements in an indecomposable sign-stable matrix A are to have opposite signs, i.e. the only type of interspecific relations in a qualitatively stable community with an indecomposable matrix are the predator-prey relations.

The following theorem (given without proof) describes the case where decomposable matrices may be sign-stable.

Theorem 1. Let $A = \| a_{ij} \|$ be a real $n \times n$ matrix with $a_{ii} < 0$ for all $i = 1, 2, \ldots, n$. Then the necessary and sufficient conditions for sign-stability of A are conditions (1) *and* (2).

Thus, at the cost of a fairly strong limitation, requiring all the species in the community be self-regulated along with the relations of the predator-prey type, amensalism and commensalism become possible.

Notice that a sign-stable matrix with a negative diagonal element is totally stable, so for matrices of such kind the diagram (4.32) may be supplemented by the relation

$$\boxed{\text{Sign-stability}} \overset{a_{ii}<0}{\Longrightarrow} \boxed{\text{Total stability}}. \tag{4.41}$$

That the relation is not reversible is shown by the example of negative definite matrix A (which is dissipative and hence, totally

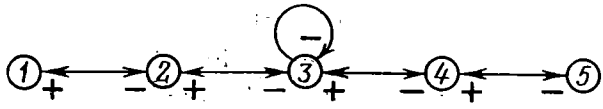

Fig. 28. SDG of a 5-species community: the 1st preys on the 2nd, the 2nd—on the 3rd and so on; the 3rd species regulates itself.

stable) with all negative elements; this matrix fails to satisfy condition (1) and cannot be sign-stable.

Consider now the matrix of a five-species community, whose SDG was presented in Fig. 28. Let

$$A = \begin{Vmatrix} 0 & 1 & 0 & 0 & 0 \\ -1 & 0 & 1 & 0 & 0 \\ 0 & -1 & -1 & 1 & 0 \\ 0 & 0 & -1 & 0 & 1 \\ 0 & 0 & 0 & -1 & 0 \end{Vmatrix}. \tag{4.42}$$

It is readily seen that A satisfies all the conditions (1)-(4) and is indecomposable, as indicated by the graph in Fig. 26. Nevertheless the spectrum of A consists of numbers $\lambda_1 \approx -0.36$, $\lambda_{2,3} = -0.32 \pm \pm 0.16i$, $\lambda_{4,5} = \pm i$, i.e. comprises pure imaginary numbers. This example demonstrates, that (1)-(4) conditions are only necessary, but not sufficient for an indecomposable matrix to be sign-stable.

The sufficient conditions discussed in the next section, indicate that for an ecosystem to be qualitatively stable not only the presence, but also the particular location of self-limiting species in the community structure is of importance.

4.7. Sufficient conditions of sign-stability

A question arises from the results and conclusions of the preceding section, could not the conditions (1)-(4) be somehow made more rigid in order to make them sufficient for sign-stability of matrix A? It turns out that condition (3) may be more rigid so that the whole combination will give sufficient conditions of sign-stability for any real, not necessarily indecomposable, matrix.

To formulate this stronger condition (3) [denote it by (3′)] we shall need the notion "of predation community". Consider a vertex in the community SDG, involved in a 2-cycle with one "+" line and one "—" line, and associate all the other vertices related to the given ones by 2-cycles of this kind; then associate with those new vertices all additional vertices related by such 2-cycles, and so on. In other words, associate into one set all the species, to form together with the given one a structure of predator-prey links. The maximal set of all such species is called the *predation community*, containing the first species. For the sake of completeness, a species not connected by + or — relations to any other species is also called a (*trivial*) predation community. If no predator-prey links occur in the community, then, by our definition, it has n trivial predation communities. SDG in Fig. 26 and in Fig. 28 contain one predation community each, whereas that in Fig. 27 has two of them: $\{1\}$ and $\{2, 3\}$.

When we split SDG with matrix $A = \| a_{ij} \|$ into predation communities, a matrix $\tilde{A} = \| \tilde{a}_{ij} \|$ may be defined as follows: $\tilde{a}_{ij} = \tilde{a}_{ij}$ if the link a_{ij} is involved in a cycle, and $a_{ij} = 0$ otherwise. For SDG and matrices satisfying conditions (1) and (2), this implies the erasure of all lines connecting predation communities (these lines belong to amensalism and commensalism relations); and matrix A becomes block-diagonal with blocks related to separate predation communities. For example, for the SDG in Fig. 27 this implies erasure of links $2 \to 1$ and $3 \to 1$, and matrix $\tilde{A}$ takes the form

$$\tilde{A} = \begin{Vmatrix} -a & 0 & 0 \\ 0 & 0 & -d \\ 0 & e & 0 \end{Vmatrix}.$$

The following Lemma indicates that the stability of the original graph is equivalent to stability of the split one.

Lemma 2. Eigenvalues of A and $\tilde{A}$ are the same.

Proof. Let the element $a_{rs} \neq 0$ be associated with a line in the graph belonging to no cycle (with more than one species). This amounts to saying that any product of elements of the form

$$a_{rs}a_{sr}, \qquad a_{ir}a_{rs}a_{si}, \qquad a_{ij}a_{jr}a_{rs}a_{si}, \ldots,$$

where $r, s, i, j, \ldots$—are different indices, becomes zero accordingly. The similar products of elements of the characteristic matrix $\| A - \lambda I \| = \| a_{ij} - \delta_{ij}\lambda \|$ turn to zero. And this implies, that the expansion of the characteristic determinant loses all terms containing the element $(a_{rs} - \delta_{rs}\lambda)$ as a factor; i.e. if we assume

that $a_{rs} = 0$, the determinant remain unchanged. Therefore

$$\det \| A - \lambda I \| = \det \| \tilde{A} - \lambda I \|, \tag{4.43}$$

Q.E.D.

Thus, the stability of predation communities characterizes the stability of the original graph. Notice, that the requirement

$$0 \neq \det A = \det \tilde{A},$$

which is obviously necessary for A to be stable, implies that all trivial predation communities should exhibit self-limitation. The stability properties of matrix $\tilde{A}$, associated with SDG partition into predation communities, are established by the following theorem.

Theorem 2. If A satisfies conditions (1)-(4), *the eigenvalues of $\tilde{A}$ have non-positive real parts, i.e.* $\operatorname{Re}\lambda(\tilde{A}) \leqslant 0$, *the multiplicity of values with zero real parts being no more than* 1.

Proof. Consider an isolated predation community of m species and the associated $m \times m$ matrix $\tilde{A}$. We define m positive constants $\alpha_1, \alpha_2, \ldots, \alpha_m$ as follows. Set $\alpha_1 = 1$. For each ith species, linked with the 1st species in $\tilde{A}$, let

$$\alpha_i = -a_{1i}/a_{i1} > 0 \tag{4.44}$$

because of condition (1) and the structure of a predation community. In exactly the same manner we define numbers α_j for each jth species linked with the ith one, from the relationship

$$\alpha_j a_{ji} = -\alpha_i a_{ij}, \quad i \neq j, \tag{4.45}$$

and so on. Because of the absence of closed loops (with more than 2 species) in the graph we thus obtain all $\alpha_1, \ldots, \alpha_m$. We define a function

$$\varphi(x_1, \ldots, x_m) = \sum_{i=1}^{m} \alpha_i x_i^2, \tag{4.46}$$

where the real m-vector $\mathbf{x}$ is the solution to the system of linear differential equations

$$d\mathbf{x}/dt = \tilde{A}\mathbf{x}. \tag{4.47}$$

The quadratic form (4.46) is obviously positive definite, and its derivative along trajectories of system (4.47) will, by (4.45), be

$$\frac{d\varphi}{dt} = 2 \sum_{i=1}^{m} \sum_{j=1}^{m} \alpha_i x_i a_{ij} x_j = 2 \sum_{i=1}^{m} \alpha_i a_{ii} x_i^2. \tag{4.48}$$

Since $a_{ii} \leqslant 0$ it follows that $d\varphi/dt \leqslant 0$, and $\varphi(x)$ is therefore a Lyapunov function for the zero solution of system (4.47), which is

thus locally stable. This suggests the statement of the theorem, for otherwise the zero solution would be unstable.

By Theorem 2, thus, only two alternatives are possible: either all Re $\lambda(\tilde{A}) < 0$, and the zero solution is asymptotically stable, or some eigenvalues of multiplicity 1 have zero real parts—the case sometimes called *neutrally stable*. The central point in what follows is to determine the conditions separating these two cases.

At det $\tilde{A} \neq 0$ the presence of purely imaginary numbers in the spectrum of $\tilde{A}$ is an alternative to asymptotic stability. The necessary condition for this is derived from the following. Each pair of purely imaginary eigenvalues of $\tilde{A}$ is related to sinusoidal terms (with a constant amplitude) in the general solution to (4.47); those components of the solution $x_i(t)$ which contain such terms will be called *oscillating*. In the predation community structure oscillating and non-oscillating species are to be specially located. In particular, species x_k with self-regulation ($a_{kk} < 0$) cannot be oscillating. In fact, for a periodic solution to system (4.47) there must be a finite closed trajectory in the phase space. Clearly, the derivative of the Lyapunov function along this trajectory $d\varphi/dt \equiv 0$, for otherwise, since $d\varphi/dt$ keeps its sign along any trajectory, the integral of $d\varphi/dt$ along the closed trajectory would be non-zero. With (4.48) and (4.44) in mind it immediately follows that $x_k \equiv 0$ everywhere along the periodic solution.

Further, considering the equation for dx_i/dt of any oscillating species x_i, it follows that x_i must be connected to at least one other oscillating species. And any non-oscillating species x_k that is connected to an oscillating species must be necessarily connected to at least one other oscillating species.

These requirements on the pattern of a neutrally stable predation community may be formalized using the "color test". A predation community is said to pass the color test provided each vertex in the associated graph may be colored *black or white* with the result that:

(a) each self-regulating vertex is black;

(b) there is at least one white vertex;

(c) each white vertex is connected by a link to at least one other white vertex; and

(d) each black vertex connected to one white vertex is connected to at least one other white vertex.

For instance, the predation community {*1*} of SDG in Fig. 27 does not satisfy the requirement (b), whereas the community {*2*, *3*} passes the test. The SDG in Fig. 28 passes the test, but if self-regulation is transferred to any other vertex, the graph will no longer pass the test.

If a predation community fails the color test, it cannot be neutrally stable, and therefore (Theorem 2) it is asymptotically stable.

Thus, if all predation communities in the original SDG associated with matrix A, fail the color test, then all $\operatorname{Re} \lambda(\tilde{A}) < 0$ and matrix A (Lemma 2) is stable.

To summarize we observe, that for any real matrix A to be sign-stable it is sufficient that the combination of conditions (1), (2), (3′) and (4) is satisfied, where (3′) requires that all self-regulating species are located in SDG in such a way that each predation community in the graph fails the color test.

4.8. Necessary and sufficient conditions of sign-stability

The examples in the previous section of violations of sufficient conditions of matrix sign-stability, as well as some other examples indicate that these sufficient conditions are "fine" enough: we could not find a single example of a sign-stable matrix A not satisfying

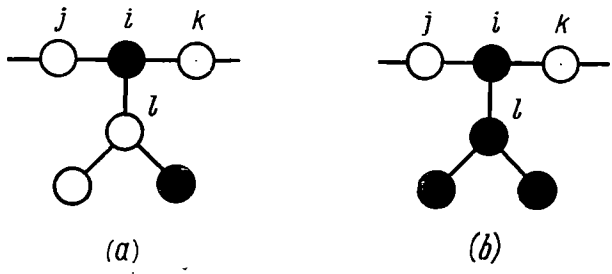

Fig. 29. An illustration to the additional condition d* of the color test.

conditions (1), (2), (3′), and (4). The reason is that these conditions turn out to be actually not only sufficient but also necessary for sign-stability of an arbitrary matrix A.

Before proving the necessity of these conditions, we introduce a notion. We will say that matrix B is equivalent to matrix A, if B and A have the same sign patterns, i.e.

$$\operatorname{sign} B = \operatorname{sign} A. \tag{4.49}$$

Then the definition of sign-stability may be stated as follows: matrix A is termed sign-stable if every equivalent matrix B is stable.

Several remarks will be of use in what follows.

Remark 1. If a predation community graph passes the color test [i.e. all the conditions (a-d) are met], then this graph passes the test with an additional restriction: (d*) each black vertex, connected with a white one, is connected exactly with two white vertices.

In fact, if a black vertex, say i in Fig. 29*a*, is connected with more than two white vertices (j, k, l in Fig. 29*a*), the "extra" white

vertices (vertex l) and the whole branches belonging to them (i.e. vertices connected with i and l), can be recolored black. Since the graph has no cycles, this recoloring does not violate the conditions a-d.

Remark 2. If a predation community graph passes the color test, it also passes the test with an additional restriction: (e) there are no "white" branches, i.e. branches originating from a white vertex, which consist of more than four vertices.

In fact, if a graph has a white branch of *5* or more vertices (as in Fig. 30*a*), the central of these vertices, as well as all the branches passing through it (if any), may be recolored black (as indicated in Fig. 30*b*), and the conditions a-d obviously remain satisfied.

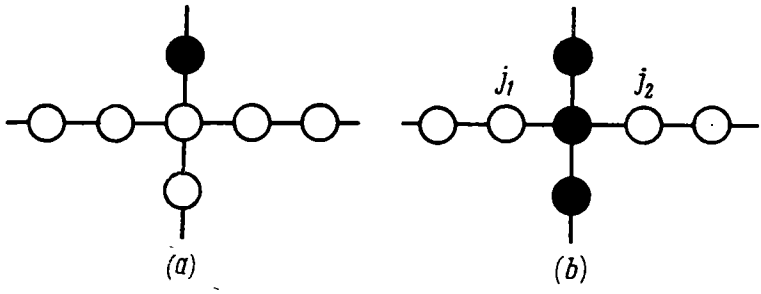

Fig. 30. An illustration to the additional condition e of the color test.

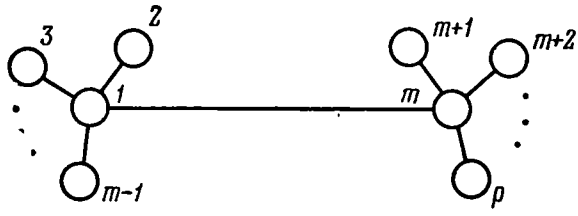

Fig. 31. Structure of the maximal connected subgraph.

According to Remarks 1 and 2 the matrix A graph may be colored so that the principles a-d*, e are satisfied. Each white vertex has a maximal "white" subgraph (i.e. a subgraph made out of white vertices), containing the given vertex. Consider all the maximal white subgraphs of the original graph. By principle (e), they should have no branches with more than 4 vertices. Therefore every maximal white subgraph appears as shown in Fig. 31.

Remark 3. Since the graph should lack closed cycles of length more than 2, two maximal subgraphs may be connected (by a branch of length 2) through one black vertex only.

Let the submatrix B of matrix A, associated with the maximal white subgraph, be produced by rows and columns with numbers $i_1, i_2, \ldots, i_p$ ($p \geqslant 2$). If we list the subgraph vertices as shown

in Fig. 31, the submatrix B will take the form

$$B = \left\| \begin{matrix} 0 & b_2 & \dots & b_{m-1} & b_m & 0 & \dots & 0 \\ c_2 & & & & 0 & & & \\ \vdots & & 0 & & \vdots & & 0 & \\ c_{m-1} & & & & 0 & & & \\ c_m & 0 & \dots & 0 & 0 & b_{m+1} & \dots & b_p \\ 0 & & & & c_{m+1} & & & \\ \vdots & & 0 & & \vdots & & 0 & \\ 0 & & & & c_p & & & \end{matrix} \right\|, \tag{4.50}$$

where $b_j c_j < 0$, $p \geqslant m \geqslant 2$.

Lemma 3. Let the conditions $b_j c_j < 0$, $p \geqslant m \geqslant 2$ hold for matrix B from (4.50). Then for all $\omega > 0$ there exists a matrix $\widetilde{B}$, equivalent to B, and having $\lambda = \pm i\omega$ for its eigenvalue. In this case the system of equations $\dot{\mathbf{x}} = \widetilde{B}\mathbf{x}$ has a particular solution of the form

$$x_j(t) = D_j \cos \omega t + E_j \sin \omega t, \quad j = 1, \dots, p, \tag{4.51}$$

where for every fixed index j_0 the variables D_{j_0} and E_{j_0} can take on arbitrary preassigned values.

Proof. Let us find the coefficients of the characteristic equation

$$\det(\lambda I - B) = \lambda^p + d_1\lambda^{p-1} + \dots + d_p = 0 \tag{4.52}$$

for matrix B of the form (4.50). Visualize for this the SDG, corresponding to the predation community graph from Fig. 31. Since there are no self-limiting species (1-cycles), and the links of preying correspond to SDG 2-cycles, we readily find the cases where the expansion of det B has non-zero terms. In fact, the graph from Fig. 31 can be partitioned into disjoint 2-cycles only when $p = 2$ or $p = 4$ ($m = 2$ or $m = 3$, respectively). Hence among all the principle minors of matrix B only those of 2nd and 4th order are distinct from zero, thus the equation (4.52) is eventually reduced to the equation

$$\lambda^p + d_2\lambda^{p-2} + d_4\lambda^{p-4} = 0. \tag{4.53}$$

Directly calculating d_2 and d_4 for matrix B from (4.50) we get

$$d_2 = \alpha + \beta + \gamma; \qquad d_4 = \alpha\gamma, \tag{4.54}$$

where

$$\begin{cases} \alpha = -b_2c_2 - \dots - b_mc_m, \\ \beta = -b_mc_m, \\ \gamma = -b_{m+1}c_{m+1} - \dots - b_pc_p. \end{cases} \tag{4.55}$$

Under the Lemma conditions the quantities α, β and γ are positive. Next we easily see that if we assume that

$$d_2 = \omega^2 + \varepsilon > 0, \; d_4 = \varepsilon\omega^2 > 0, \tag{4.56}$$

where $\omega > 0$ is a preassigned number, the numbers $\lambda = \pm i\omega$ are roots of (4.53). Therefore it is sufficient to choose positive numbers α, β, γ and ε such that equations (4.56) and (4.54) hold, and to choose the elements $\tilde{b}_j$ and $\tilde{c}_j$ of the desired matrix $\tilde{B}$ so that they will satisfy equations similar to (4.55), and then numbers $\lambda = \pm i\omega$ will be eigenvalues for matrix $\tilde{B}$, equivalent to B. This proves the first part of Lemma 3 statement.

Denote the eigenvectors of $\tilde{B}$, belonging to $\lambda = \pm i\omega$ by $\mathbf{z} = \boldsymbol{\eta} - i\boldsymbol{\zeta}$ and $\bar{\mathbf{z}} = \boldsymbol{\eta} - i\boldsymbol{\zeta}$. Then among the solutions to system $\dot{\mathbf{x}} = \tilde{B}\mathbf{x}$ there is a solution of the form

$$\mathbf{x}(t) = C\mathbf{z}\exp\{i\omega t\} + \overline{C\mathbf{z}}\exp\{-i\omega t\}, \quad \mathbf{x} \in R^p \tag{4.57}$$

where $C = C_1 + iC_2$ is an arbitrary complex constant.

It can be easily shown that the solution (4.57) coincides with

$$\mathbf{x}(t) = \mathbf{D}\cos\omega t + \mathbf{E}\sin\omega t, \tag{4.58}$$

where

$$\begin{cases} \mathbf{D} = 2(C_1\boldsymbol{\eta} - C_2\boldsymbol{\zeta}) \\ \mathbf{E} = -2(C_1\boldsymbol{\zeta} + C_2\boldsymbol{\eta}). \end{cases} \tag{4.59}$$

For every fixed index j_0, from (4.59) we have system of equations

$$\begin{cases} 2(\eta_{j_0}C_1 - \zeta_{j_0}C_2) = D_{j_0}, \\ -2(\zeta_{j_0}C_1 + \eta_{j_0}C_2) = E_{j_0}, \end{cases} \tag{4.60}$$

which for given D_{j_0} and E_{j_0} uniquely determines C_1 and C_2 values and hence the sought particular solution (4.58), provided only that its determinant is distinct from zero.

Suppose the opposite, i.e. that

$$-4(\eta_{j_0}^2 + \zeta_{j_0}^2) = 0.$$

Then $\eta_{j_0} = \zeta_{j_0} = 0$ and $x_{j_0}(t) \equiv 0$. Recall now that matrix B by its structure is a matrix of the maximal white subgraph, satisfying in particular the principle (d) (cf. Remark *2*). For the system $\dot{\mathbf{x}} = \tilde{B}\mathbf{x}$ to have the oscillating solution (4.58) with the non-oscillating component x_{j_0}, a version of the graph coloring must exist, such that the non-oscillating components belong to black vertices, whereas the result passes the color test. However, it is readily seen that the recoloring of any white vertex of the graph in Fig. 31 results in failing the test, therefore the oscillating solution (4.58) cannot

have an identically zero component x_{j_0}. The obtained contradiction concludes the proof of Lemma 3.

By Lemma 2 of the preceding section the sign-stability of all predation subcommunities is the sufficient and necessary condition of the community matrix sign-stability. The necessary condition of sign-stability for one predation community, or in matrix terms, of sign-stability of an indecomposable matrix with a symmetric structure of zeros and non-zeros is provided by:

Theorem 3. If a predation community matrix A is sign-stable, the corresponding graph fails the color test.

Proof. In the case of a trivial predation community, i.e. an isolated species, the theorem statement is obvious, since a graph of one black vertex fails the (b) rule of the color test.

In a non-trivial case, we assume the opposite, i.e. that the matrix A graph passes the color test, and show that then a matrix $\tilde{A}$ exists, equivalent to A in terms of (4.49) such that the system of equations

$$\dot{\mathbf{x}} = \tilde{A}\mathbf{x}, \qquad \mathbf{x} \in R^n, \tag{4.61}$$

has a solution with oscillating components. In other words, matrix $\tilde{A}$ is not stable and therefore matrix A cannot be sign-stable.

Consider the maximal white subgraphs of matrix A. By Lemma 3 we can alter the absolute values of A elements in such a way that every submatrix B, related to a separate maximal white subgraph, will generate for the subsystem $\dot{\mathbf{x}} = \tilde{B}\mathbf{x}$ a solution of the (4.58) form, with the value $\omega > 0$ identical for all submatrices $\tilde{B}$. This can be done since the maximal white subgraphs are disjoint. The matrix obtained we denote by $\tilde{A}$ and show that in this case an oscillating solution to the full system (4.61) exists. This solution may be constructed, using solutions of the form for each "white" component and assuming all "black" components to be identically zero.

In fact, system (4.61) may be rewritten in the form

$$\dot{x}_k = \sum_{j=1}^{n} \tilde{a}_{kj} x_j(t), \qquad k = 1, \ldots, n, \tag{4.62}$$

where $\tilde{a}_{kj} \neq 0$ if and only if the vertices k and j are connected by a predation link. Since all the black components are zero, only the white components j linked with vertex k contribute to the sum (4.62). Therefore if k is a white component, the equation (4.62) merely coincides with the corresponding equations of the subsystem $\dot{\mathbf{x}} = \tilde{B}\mathbf{x}$ and is naturally satisfied by the solution $x_k(t)$ of the form (4.58). If vertex k is black, by the principle (**d***) either there are no non-zero terms in the sum (4.62) at all (when the black vertex is linked with not a single white one), or there are exactly two non-zero terms, appearing when white vertices, say j_1 and j_2, are linked

with the black vertex k. In the first case (4.62) is obviously satisfied, and in the second

$$0 \equiv \dot{x}_k = \tilde{a}_{kj_1} x_{j_1}(t) + \tilde{a}_{kj_2} x_{j_2}(t)$$

$$= \tilde{a}_{kj_1}(D_{j_1} \cos \omega t + E_{j_1} \sin \omega t) + \tilde{a}_{kj_2}(D_{j_2} \cos \omega t + E_{j_2} \sin \omega t). \qquad (4.63)$$

Since the graph has no cycles, the vertices j_1 and j_2 belong to different maximal white subgraphs. By Lemma 3 the values D_{j_2} and E_{j_2} can then be chosen (without altering the elements $\tilde{a}_{ij}$) equal to

$$D_{j_2} = -\tilde{a}_{kj_1} D_{j_1} / \tilde{a}_{kj_2}, \qquad E_{j_2} = -\tilde{a}_{kj_1} E_{j_1} / \tilde{a}_{kj_2} \qquad (4.64)$$

with the result that the right-hand side of (4.63) becomes identically zero.

According to Remark 3, two maximal white subgraphs can only be connected through one black vertex. Therefore, starting from one maximal white subgraph, we can sort out all the other subgraphs of the given predation community "sewing" together the solutions to all subsystems $\dot{\mathbf{x}} = \tilde{B}\mathbf{x}$ by formulas (4.64) into an oscillating solution to the full system (4.61). Theorem 3 is proved.

* * *

The results of the two previous sections enable us to formulate the sign-stability criterion for an arbitrary matrix A:

For sign-stability of an arbitrary matrix A it is necessary and sufficient that matrix A satisfies conditions 1, 2, 4 and that the graph of each of its predation communities fails the color test.

Describing the class of qualitatively stable communities with this criterion in mind, we find that it consists:

either of predation communities, i.e. structures with a single type of predator-prey pair interactions (including in that case types such as resource-consumer, host-parasite, etc.), and with specifically positioned self-limiting species, failing the color test;

or of several similar communities, with relations of amensalism and commensalism possible among their different species, provided that they do not form closed directed cycles in a complete community structure.

Notice that the class of qualitatively stable communities turns out to be quite narrow. In particular, it does not embrace competitive communities, as well as structures reflecting closed substances cycles, common in real ecosystem modeling.

Nevertheless, sign-stability analysis of natural ecosystems is a fairly simple means of deriving some information about their

structure from the viewpoint of stability; this analysis can identify, for instance, those species whose position in the community structure is of critical importance for the stability of the whole system.

The notion of community qualitative stability was reduced to sign-stability of the community matrix on the basis of the Lyapunov stability of the non-trivial equilibrium in the appropriate model. However, stable species can coexist even when the equilibrium point is not stable, e.g. when populations demonstrate oscillations with bounded amplitudes. Therefore the following question is of particular interest both from the ecological and mathematical points of view: to what extent can we extend the class of qualitatively stable communities if we relax the requirement of the Lyapunov stability and replace it by some analogy of ecological stability.

The lack of qualitative stability, however, does not imply, that the system cannot be stable in some domains of the parameter values—these are just the cases considered in the following chapters.

4.9. Notes and bibliography

To 4.1. The species interaction types are classed on the basis of the pair of signs of mutual influence in the book (apart from the fundamental monograph by E. Odum):

Williamson M., *The analysis of biological populations*, Edward Arnold, London, 1972.

To 4.2 and 4.3. The results of V. Volterra on conservative and dissipative communities are presented in his lectures:

Volterra V., *Lecons sur la théorie mathématique de la lutte pour la vie*, Gauthier-Villars et Cie, éditeurs, Paris, 1931.

The postscript to the Russian translation of this book:

Svirezhev Yu. M., Vito Volterra and the modern mathematical ecology. In: Volterra V. *Mathematical theory of struggle for existence*, (in Russian), Nauka, Moscow, 1976,

contains the material of Section 2.

To 4.4. The results are taken from

Yorke J. A., Anderson W. N., "Predator-prey patterns," *Proc. Nat. Acad. Sci. USA*, **70**, 7, pp. 2069-2071, 1973.

An algorithm to find a pairing of maximum cardinality is presented in the paper:

Edmonds J., "Paths, trees, and flowers," *Can. J. Math.*, **17**, 3, pp. 449-467, 1965.

In the literature on graph theory, a predator-prey pairing is termed a matching, and a trophic graph is called bipartite or simple.

To 4.5. The definition of D-stability and total stability of a matrix as well as the necessary condition of D-stability follow the paper:

Quirk J. P., Ruppert R., "Qualitative economics and the stability of equilibrium," *Rev. Econ. Studies*, **32**, 92, pp. 311-326, 1965.

In a somewhat different but equivalent form the definition of D-stability is given in the work:

Arrow K. J., MacManus M., "A note on dynamic stability," *Econometrika*, **26**, 3, pp. 448-454, 1958.

The sufficient condition of D-stability is proved here as well.

To 4.6 and 4.7. The notion of qualitative stability of a community was stated and discussed in the works:

May R. M., "Qualitative stability in model ecosystems," *Ecology*, **54**, 3, pp. 638-641, 1973;

May R. M., "Stability and complexity in model ecosystems," Princeton Univ. Press, Princeton, 1973.

The definition of matrix sign stability, conditions (1)-(4) and a number of theorems about sign stability, Theorem 1 included, may be found in the above-mentioned paper by Quirk and Ruppert*. The basic insights into the proof of Lemma 1 are also taken from there.

Examples of unstable matrices (4.40) and (4.42) and the proof of sufficient conditions of sign stability were proposed in the paper:

Jeffries C., "Qualitative stability and diagraphs in model ecosystems," *Ecology*, 55, 6, pp. 1415-1419, 1974.

For those interested in the generalization of these conditions to the case where elements of matrix A are functions of population numbers and t, we recommend

Jeffries C., "Stability of ecosystems with complex food webs," *Theor. Pop. Biol.*, 7, 2, pp. 149-155, 1975.

Further analysis of community qualitative properties with the help of signed directed graphs may be found in the paper:

Levins R., "Evolution in communities near equilibrium," In: "*Ecology and evolution of communities*," Eds. M. Cody, J. Diamond, Harward Univ. Press, Cambridge, pp. 16-50, 1975.

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* Conditions (1)-(4) are erroneously announced here to be sufficient for sign stability of an indecomposable matrix.

CHAPTER 5

TROPHIC CHAINS AND COMMUNITIES WITH VERTICAL STRUCTURE

5.1. Ecological introduction

The community structure, presenting the transfer of energy trapped in food from one species to another (linked together by predator-prey type relations), is known in ecology as the *trophic chain*. In every successive transfer a significant part of energy (70-80%) is lost, being spent on respiration and heat. This restricts the number of "links" in the chain usually to four-five, though in all ecosystems either always exist (if only in negligible numbers), or are introduced from outside, the specimens which could form the next trophic level. When the amount of energy coming into the ecosystem sharply increases or the first level productivity grows significantly under effects of some kind (for instance, fertilizer application), the possibility of the new level formation, using the generation material available, is realized and a new trophic level appears and establishes itself in the system.

Trophic chains are not isolated from each other and, interweaving, they form a trophic graph (trophic web). An example of such a trophic web (an ecosystem of a small stream) is displayed in Fig. 32. It is an open ecosystem with a part of the basic resource comming with fallen leaves *1* and other organic residues *2*, carried by the flow. The system comprises three trophic levels. The species *3*—green algae and *4*—diatomes make up the producers level; species *5*—*Protonemura*, *6*—blackflies and nonbiting midges, *7*—caddisfly (*Philopotamus*), and *8*—mayfly (*Ecdyonurus*) constitute the level of primary consumers, and species *11*—stonefly (*Perla*) and *12*—caddisfly (*Dinocras*), the secondary consumers level. The species *9*—caddisflies, which build a catching net, and *10*—the caddisfly *Rhyacophila*, occupy an interstitial level. Evidently, the sequences of species $3 \rightarrow 6 \rightarrow 12$ or $2 \rightarrow 7 \rightarrow 11$ form trophic chains (other examples may be cited).

It can be said that a trophic chain presents a community, in which every two adjacent species make up a predator-prey pair; whereas the trophic chain originates from a resource of some kind. It is only natural to call such a community a *vertically structured community*.

Any real community is described by a fairly complicated trophic web, and the model becomes complicated too. Apparently, there are two ways to make the original model more simple. Either to aggregate all the species of the same trophic level into one "pseudo-species", or to distinguish one vertical branch (one trophic chain) in the trophic web, with the largest energy flow, and neglect all the other chains. The first method may be used, when species in one trophic level are close in their ecological characteristics, and

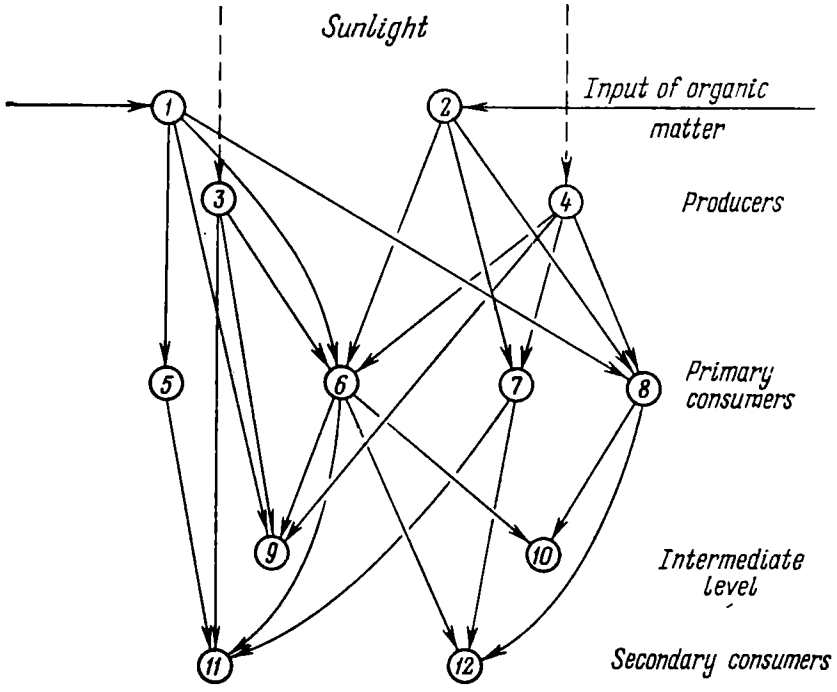

Fig. 32. Part of a trophic web in a stream ecosystem in South Wales. (From: Jones J. R. E., "A further ecological study of a calcareous stream in the "Black Mountain" district of South Wales," *J. Anim. Ecol.*, 18, 2, pp. 142-159, 1949.)

the "pseudo-species" is then a species with averaged characteristics. The second method is advisable, when a dominant species may be distinguished in each trophic level. In any case, these simplifying operations leave one species in each level, and the trophic structure of this aggregated community will be described by a trophic chain. But when the averaging or the choice of a dominant species in one trophic level is impossible (for instance, if there exist two or more markedly different but energetically equal ecological groups), a number of trophic branches or branching trophic chains are to be considered.

The present chapter is concerned with stability analysis of such trophic patterns within the framework of "almost-Volterra" models.

5.2. Closed and open trophic chains

So far we did not define the notion of "resource". In real ecosystems it may be either energy, or vitally important substances of some kind (say, carbon, nitrogen, or phosphorus). While in reference to energy any ecosystem is open, the sunlight energy "flowing" through the ecosystem and dispersing at the same time as heat (respiration, vital activity, etc.), in reference to biological substances (carbon, nitrogen phosphorus, etc.), ecosystems are always closed

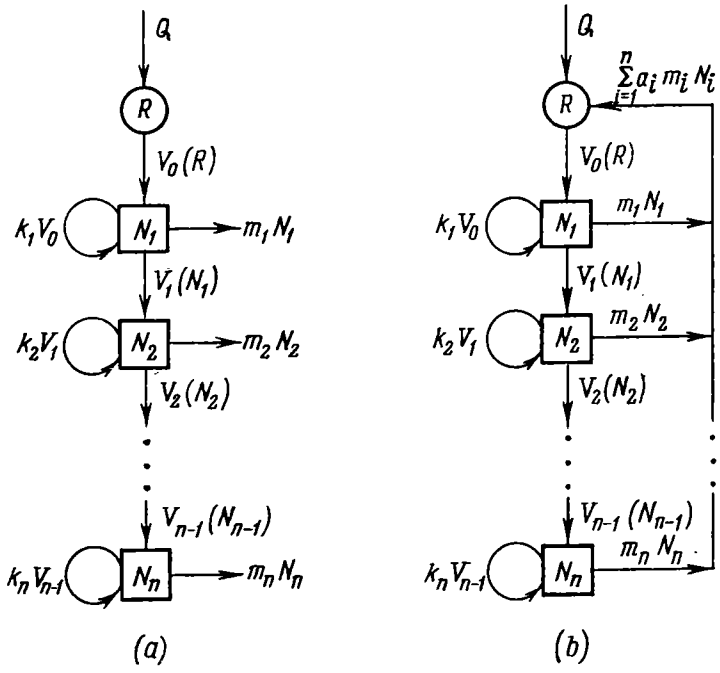

Fig. 33. Trophic chains with n members: (a) open ("flow-through") chain; (b) closed chain ("cycle"). The coefficients a_i ($0 \leqslant a_i \leqslant 1$) are the fractions of the resource reproduced by the destructors present in the dead biomass of the ith species. These coefficients specify the degree of closure in the trophic chain.

to a certain extent. The closing is performed by the so-called "decomposers" (microorganisms, funga, worms), which decompose dead organic material into mineral components, thus providing nutrients to the primary trophic levels. The same is true of trophic chains. Therefore, in what follows trophic chains of two types will be considered: open (flow-through) and closed ("cyclic"). Both types are depicted in Fig. 33.

The ecosystem growth and development is generally limited by one factor (*Liebig principle*). This may be either sunlight, or some chemical element, usually nitrogen or phosphorus. While sunlight is an unrenewable resource, the chemical substances are reinvolved

in the cycle through decomposer activity. Therefore, when sunlight is a limiting factor, the trophic chain is open, whereas if a nutrient is limiting, the chain forms a closed loop.

Consider in more details the diagrams in Fig. 33. Here R is a resource, consumed by a first species of biomass N_1. The specific rate of uptake $V_0(R)$ is the amount of resource consumed by a unit biomass of the first species (one specimen) in a unit time. From the total amount of the consumed resource, $V_0(R)$, only the k_1th fraction goes into the reproduction of the 1st species biomass, the rest being spent to maintain vital activity. In addition, the 1st species biomass dies at a constant rate m_1, it serves as a resource for a 2nd species and is consumed at a specific rate $V_1(N_1)$, a 3rd species uptakes the biomass of the 2nd, and so on. The chain comes to an end with the nth species, whose biomass nobody uptakes.

The second diagram in this figure differs from the first in that there exists an $(n+1)$th species—the decomposer, which utilizes the dead biomass of the first n species as a resource and through its vital activity makes up in part for the loss of resource R. We shall assume that the dead biomass decomposition is performed quickly enough and the released resource becomes available for the 1st species practically at once. Moreover, the growth rate of the decomposer biomass is assumed to be so high, that it can utilize any amount of dead biomass practically at once. In this case there is no use to consider the population or biomass of the decomposer-species as a separate phase variable. All the dying biomass (or a fraction of it, if we take into account the losses inevitable in the process) may be considered to return instantaneously to the resource block.

Let the trophic graph of the ecosystem be of the type shown in Fig. 33. Suppose that the whole ecosystem thus organized approaches some state of equilibrium, the steady state populations of only the first q species being non-zero. This stable equilibrium is naturally termed a *trophic chain of q members.*

Let the supply rate of the external resource to the ecosystem be constant and equal to Q. The problem is stated as follows: what this rate should be (for given trophic functions $V_0(R)$, $V_i(N_i)$, $i = 1, \ldots, n$, and parameters k_i, m_i, a_i) for this community to have a stable non-trivial equilibrium with non-zero populations of the first q species? In other words, what are the conditions for a trophic chain of q members to exist? Obviously, these conditions are determined by ecosystem parameters and the flow rate of the external resource into the ecosystem.

According to the trophic graphs in Fig. 33 the following mass-balance equations for species may be written easily enough.

(a) *Open chain*

$$\begin{aligned}
\frac{dR}{dt} &= Q - V_0(R)\,N_1,\\
\frac{dN_1}{dt} &= -m_1N_1 + k_1V_0(R)\,N_1 - V_1(N_1)\,N_2,\\
\frac{dN_i}{dt} &= -m_iN_i + k_iV_{i-1}(N_{i-1})\,N_i - V_i(N_i)\,N_{i+1},\\
&\qquad\qquad i = 2,\ 3,\ \ldots,\ n-1,\\
\frac{dN_n}{dt} &= -m_nN_n + k_nV_{n-1}(N_{n-1})\,N_n.
\end{aligned} \tag{5.1}$$

(b) *Closed chain*:

$$\begin{aligned}
\frac{dR}{dt} &= Q - V_0(R)\,N_1 + \sum_{i=1}^{n} a_im_iN_i,\\
\frac{dN_1}{dt} &= -m_1N_1 + k_1V_0(R)\,N_1 - V_1(N_1)\,N_2,\\
\frac{dN_i}{dt} &= -m_iN_i + k_iV_{i-1}(N_{i-1})\,N_i - V_i(N_i)\,N_{i+1},\\
&\qquad\qquad i = 2,\ 3,\ \ldots,\ n-1,\\
\frac{dN_n}{dt} &= -m_nN_n + k_nV_{n-1}(N_{n-1})\,N_n.
\end{aligned} \tag{5.2}$$

By their biological nature the parameters k_i and a_i meet the restrictions $0 \leqslant k_i \leqslant 1$, $0 \leqslant a_i \leqslant 1$.

If we assume, that no species is excessively supplied by the resource, i.e. that the trophic links are "strained" (cf. Section 3.2), then we can take

$$V_0(R) = \alpha_0R,\ V_i(N_i) = \alpha_iN_i \quad (i = 1,\ \ldots,\ n) \tag{5.3}$$

and the equations (5.1) and (5.2) are transformed into the Volterra-type equations (excluding the first equations, which have the term Q). Then, formally assuming that $R \equiv N_0$ and $N_{n+1} \equiv 0$ we get the following two systems to account for dynamics in trophic chains of the two types.

(a) *Open chain*:

$$\begin{aligned}
\frac{dN_0}{dt} &= Q - \alpha_0N_0N_1,\\
\frac{dN_i}{dt} &= N_i(-m_i + k_i\alpha_{i-1}N_{i-1} - \alpha_iN_{i+1}), \qquad i = 1,\ \ldots,\ n.
\end{aligned} \tag{5.4}$$

(b) *Closed chain*:

$$\begin{aligned}
\frac{dN_0}{dt} &= Q - \alpha_0N_0N_1 + \sum_{i=1}^{n} a_im_iN_i,\\
\frac{dN_i}{dt} &= N_i(-m_i + k_i\alpha_{i-1}N_{i-1} - \alpha_iN_{i+1}), \qquad i = 1,\ \ldots,\ n.
\end{aligned} \tag{5.5}$$

Conditions of existence and stability of equilibrium in these systems, i.e. conditions for trophic chains to exist, are to be considered in the following sections.

5.3. Equilibria in open chain

In a system characterized by equation (5.4), for $Q > 0$, n equilibria of the form $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ may exist, where N_i^* appears from equations

$$N_1^* = \frac{Q}{\alpha_0 N_0^*}, \qquad \alpha_i N_{i+1}^* = k_i \alpha_{i-1} N_{i-1}^* - m_i, \qquad i = 1, \ldots, q. \tag{5.6}$$

From the condition $N_{q+1}^* = 0$ it immediately follows that

$$N_{q-1}^* = \frac{m_q}{\alpha_{q-1} k_q}. \tag{5.7}$$

The remaining N_i^* values may be easily obtained by induction:

$$N_{2s}^* = H_{2s-1}(N_0^* - f_{2s-1}), \qquad N_{2s+1}^* = H_{2s}(N_1^* - f_{2s}). \qquad s = 1, 2, \ldots, \tag{5.8}$$

where

$$H_{2s-1} = g_1 g_3 \ldots g_{2s-1}, \qquad H_{2s} = g_2 g_4 \ldots g_{2s}, \qquad g_i = k_i \alpha_{i-1}/\alpha_i, \qquad i = 1, \ldots, n; \tag{5.9}$$

$$f_{2s-1} = \frac{\mu_1}{H_1} + \frac{\mu_3}{H_3} + \ldots + \frac{\mu_{2s-1}}{H_{2s-1}}, \qquad f_{2s} = \frac{\mu_2}{H_2} + \frac{\mu_3}{H_4} + \ldots + \frac{\mu_{2s}}{H_{2s}}, \qquad \mu_i = m_i/\alpha_i, \qquad i = 1, \ldots, n. \tag{5.10}$$

It is apparent from these expressions alone, that the steady values of species populations depend upon the evenness of their numbers. Therefore two cases are worth considering.

1. Let $q = 2S$ be *even*. Then

$$N_{q-1}^* = N_{2S-1}^* = \frac{\mu_{2S}}{g_{2S}} = H_{2S-2}(N_1^* - f_{2S-2}),$$

whence it immediately follows that

$$N_1^* = f_{2S-2} + \frac{\mu_{2S}}{g_{2S} H_{2S-2}} = f_{2S-2} + \frac{\mu_{2S}}{H_{2S}} = f_{2S}.$$

Using the first equation in (5.6) we get

$$N_0^* = \frac{Q}{\alpha_0 N_1^*} = \frac{Q}{\alpha_0 f_{2S}}.$$

Knowing how N_0^* and N_1^* are expressed in termes of system parameters, by formula (5.8) explicit relationships for the stationary

population of any species may be easily obtained; for instance,

$$N_q^* = N_{2S}^* = H_{2S-1}\left(\frac{Q}{\alpha_0 f_{2S}} - f_{2S-1}\right). \tag{5.11}$$

2. Let $q = 2S + 1$ be *odd*. In a like manner we get

$$N_{q-1}^* = N_{2S}^* = \frac{\mu_{2S+1}}{g_{2S+1}} = H_{2S-1}(N_0^* - f_{2S-1}),$$

hence

$$N_0^* = f_{2S+1}, \qquad N_1^* = Q/(\alpha_0 f_{2S+1}),$$

$$N_q^* = N_{2S+1}^* = H_{2S}\left(\frac{Q}{\alpha_0 f_{2S+1}} - f_{2S}\right). \tag{5.12}$$

Obviously, the steady-state populations N_i^* have sense only if they are positive. Consider this point in more detail.

By definition, the functions f_{2s-1} and f_{2s} are positive and grow with s. Variables N_0^* and N_1^* are also positive and are related to the parameter q—the "length" of the trophic chain. Prove that the inequalities

$$Q > \alpha_0 f_{2S-1} f_{2S} \qquad (q = 2S), \tag{5.13}$$

or

$$Q > \alpha_0 f_{2S} f_{2S+1} \qquad (q = 2S + 1), \tag{5.14}$$

i.e. $N_q^* > 0$, imply that all the preceding N_i^* $(i = 1, \ldots, q - 1)$ should be positive as well.

The proof is easily carried out from the opposite. But before proceeding with the proof, notice, that by (5.7) always $N_{q-1}^* > 0$.

Suppose that, for some $q' < q$, $N_{q'}^* \leqslant 0$. There might be four alternatives: either q and q' are both even or both are odd, either q is even and q is odd, or vice versa.

Let $q = 2S$ and $q' = 2S'$ $(S' < S)$, that is, both are even. Then from (5.8) it follows that $N_{2S'}^* \leqslant 0$ if $N_0^* \leqslant f_{2S'-1}$. But $q = 2S$ $N_0^* = Q/(\alpha_0 f_{2S})$ and the condition $N_{2S'}^* \leqslant 0$ is met if only the inequality $Q \leqslant \alpha_0 f_{2S'-1} f_{2S}$ is satisfied. Comparing this inequality with (5.13), we obtain

$$\alpha_0 f_{2S-1} f_{2S} < Q \leqslant \alpha_0 f_{2S'-1} f_{2S},$$

or

$$f_{2S-1} < f_{2S'-1}.$$

But this is impossible, since f_{2S-1} steadily grows with s. Now let $q = 2S$ and $q' = 2S' + 1$ $(2S' < 2S - 1)$. Then from (5.8) it follows that $N_{2S'+1}^* \leqslant 0$ for $N_1^* \leqslant f_{2S'}$. This inequality is again impossible due to the steady growth of f_{2S} with S.

For odd q, similar arguments prove our statement.

At first sight, the proved statement seems obvious. In fact, if some species population is non-zero, all the more should be non-zero the populations of species placed above in the trophic chain, since the species considered actually preys on their biomass. However, this obvious statement in no way follows from our models, which formally may admit the existence of negative populations as well.

Notice that inequalities (5.13) and (5.14) place certain restrictions on the flow rate of the external resource into the system. It may be said that if there are q members in a trophic chain, the flow rate of the resource must exceed some threshold value $Q^*(q) = \alpha_0 f_{q-1} f_q$.

In this section we shall briefly examine the problem of the existence of "paradoxical" trophic chains. They may be called "paradoxical" because steady populations or biomasses in the higher trophic levels are less than in the lower ones. In the extreme case this implies

$$N_1^* < N_2^* < \ldots < N_q^*. \tag{5.15}$$

Less pronounced cases are possible, when N_i^* first increase with the number i but afterwards begin to decline. Such paradoxical trophic chains are observed in real ecosystems. But can they exist in our model? To answer this question one may write down the chain of inequalities (5.15), incorporating the obtained explicit expressions for N_i^* in terms of system parameters; however, this result is hard to interpret. Therefore, we restrict ourselves to the study of two particular cases, that is, when $q = 2$ (even number of species) and $q = 3$ (odd number).

Let $q = 2$ ($S = 1$). Then for $N_1^* < N_2^*$ it is necessary that

$$f_2 < H_1 \left(\frac{Q}{\alpha_0 f_2} - f_1 \right), \tag{5.16}$$

or

$$Q > \alpha_0 f_1 f_2 + \frac{\alpha_0 f_2^2}{H_1}. \tag{5.17}$$

Here we utilized the formula (5.11) with $S = 1$. Comparing the inequalities (5.17) and (5.13) (with $S = 1$), we see that in a paradoxical trophic chain the supply rate of the external resource should be higher than in an ordinary chain.

Let $q = 3$ ($S = 1$). Then for the inequalities $N_1^* < N_2^* < N_3^*$ to hold it is necessary that [cf. (5.12)]

$$\frac{Q}{\alpha_0 f_3} < H_1 (f_3 - f_1) < H_2 \left(\frac{Q}{\alpha_0 f_3} - f_2 \right), \tag{5.18}$$

or

$$\alpha_0 f_2 f_3 + \frac{\alpha_0 H_1 (f_3 - f_1)}{H_2} < Q < \alpha_0 H_1 f_3 (f_3 - f_1). \tag{5.19}$$

And here again, as in the preceeding case, the supply rate of the external resource is higher in the paradoxical chain, being however bounded above.

To sum up, inequalities (5.13) and (5.14) are far from being sufficient for the existence of an open trophic chain with q members, since the fact that the steady populations N_i^* of the first q species in the system are positive does not necessarily suggest the stability of this equilibrium. Therefore, in order to check the existence of a q-member trophic chain, it is necessary to find conditions which make the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ stable.

5.4. Equilibria in closed chain

In system (5.5) describing ecosystem dynamics with a partial renewal of the resource, n equilibria of the type $[N_0, N_1, \ldots, N_q, 0, \ldots, 0]$ $(q = 1, \ldots, n)$ may also exist. Stationary populations N_i^* can be found from the equations

$$\begin{aligned} &Q + \sum_{i=1}^{n} a_i m_i N_i^* = \alpha_0 N_0^* N_1^*, \\ &\alpha_i N_{i+1}^* = k_i \alpha_{i-1} N_{i-1}^* - m_i, \qquad i = 1, \ldots, q, \\ &N_{q+1}^* = 0. \end{aligned} \tag{5.20}$$

Arguing along the same line as in the preceeding section we can get the explicit expressions for N_i^* in terms of system parameters. If the explicit expressions for N_0^* and N_1^* are known, the rest of N_i^* may be found from formulas (5.8).

1. Let $q = 2S$ be *even*. Then

$$\begin{aligned} &N_1^* = f_{2S}, \\ &N_0^* = \frac{Q + (f_{2S}\psi_S - \sigma_{2S})}{\alpha_0 f_{2S} - \varphi_S}. \end{aligned} \tag{5.21}$$

Here

$$\varphi_S = \sum_{j=1}^{S} a_{2j} m_{2j} H_{2j-1}, \qquad \psi_S = \sum_{j=1}^{S} a_{2j-1} m_{2j-1} H_{2j-2},$$

$$\sigma_{2S} = \sum_{j=1}^{2S} a_j m_j f_{j-1} H_{j-1} \qquad (H_0 = 1,\ f_0 = 0).$$

2. Let $q = 2S + 1$ be *odd*. Then

$$\begin{aligned} &N_0^* = f_{2S+1}, \\ &N_1^* = \frac{Q + (f_{2S+1}\varphi_S - \sigma_{2S+1})}{\alpha_0 f_{2S+1} - \psi_{S+1}}. \end{aligned} \tag{5.22}$$

It is again easy to prove (like in Section 3), that if $N_q^* > 0$, all the previous N_i^* are positive. The condition that N_q^* is positive sets

a lower bound on the supply rate Q of the external resource. In fact, from (5.8) for $s = S$ it follows that

1. $q = 2S, \qquad N_q^* = H_{2S-1}(N_0^* - f_{2S-1}) > 0.$
2. $q = 2S + 1, \qquad N_q^* = H_{2S}(N_1^* - f_{2S}) > 0.$

Substituting from (5.21) and (5.22) the expressions for N_0^* and N_1^* in these inequalities and solving them for Q, we get

$$Q > \alpha_0 f_{2S-1} f_{2S} - \{(f_{2S-1}\varphi_S + f_{2S}\psi_S) - \sigma_{2S}\} = \widetilde{Q}^*(q) \quad (q = 2S) \tag{5.23}$$

or

$$Q > \alpha_0 f_{2S} f_{2S+1} - \{(f_{2S}\psi_{S+1} + f_{2S+1}\varphi_S) - \sigma_{2S+1}\} = \widetilde{Q}^*(q)$$
$$(q = 2S + 1). \tag{5.24}$$

Inequalities (5.23) and (5.24) give the lower bounds on the resource supply rate. It can be shown that the expressions in braces are always positive. This indicates that if an open chain is compaired with a closed one of the same length, the closed chain may have a lower supply rate of the external resource than the open one (generally, this is natural, since the resource is partially renewed in the first case).

In conclusion, we notice that as in the preceding section it still remains to be seen whether this equilibrium state is stable.

5.5. Conditions of existence of open trophic chain of constant length

The problem of stability of the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ is reduced to the analysis of eigenvalue of the matrix of system (5.4) linearized in the neighborhood of the equilibrium. But before we proceed to tackle this problem, let us prove one useful statement.

Suppose we have a $(q + 1) \times (q + 1)$ matrix A_q of the form (the so-called *Jacobian* matrix):

$$A_q = \| a_{ij} \| = \begin{Vmatrix} -b_0 & -d_0 & & & 0 & \\ b_1 & -h_1 & -d_1 & & & \\ \cdot & \cdot & \cdot & & & \\ & \cdot & \cdot & \cdot & & \\ & & \cdot & \cdot & \cdot & \\ 0 & & b_{q-1} & -h_{q-1} & -d_{q-1} \\ & & & b_q & -h_q \end{Vmatrix}, \tag{5.25}$$

where all b_i and d_i are positive and h_i are negative. Then SDG associated with the Jacobian matrix A_q (cf. Section 4.6) is of the form illustrated in Fig. 34.

In this graph:

(1) all oppositely directed links have opposite signs ($a_{ij}a_{ji} < 0$);

(2) there are no directed cycles with 3 or more species;

(3) all the vertices constitute one predation community, which can be easily shown to fail the color test for any version of broken lines (any set of $h_i \geqslant 0$), and,

(4) the partition into cycles, which corresponds to a non-zero term of the A_q determinant is given by the vertices $\{0\}$; $\{1, 2\}$; . . . . . .; $\{q-1, q\}$ when q is even, and by vertices $\{0, 1\}$; $\{2, 3\}$; . . . . . .; $\{q-1, q\}$, when q is odd.

Thus matrix A_q meets the sufficient conditions of sign stability (Section 4.7), therefore A_q is stable for any values $b, d_i > 0$ and $h_i \geqslant \geqslant 0$.

Returning now to our problem, we see that the matrix of system (5.4), which has been linearized in the neighborhood of the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$, has the following pattern:

$$F = \begin{Vmatrix} A_q & 0 \\ 0 & D_{n-q} \end{Vmatrix}, \tag{5.26}$$

where A_q is a Jacobian matrix of the type of (5.25) with elements

$$b_0 = \alpha_0 N_1^*, \qquad b_i = k_i \alpha_{i-1} N_i^*,$$
$$d_0 = \alpha_0 N_0^*, \qquad d_i = \alpha_i N_i^*,$$
$$h_i = 0, \qquad i = 1, \ldots, q,$$
$$D_{n-q} = \operatorname{diag}\{-m_{q+1} + k_{q+1}\alpha_q N_q^*, -m_{q+2}, \ldots, -m_n\}.$$

The eigenvalues for F are

$$\lambda_i = \begin{cases} \mu_i, \ i = 0, \ldots, q, \text{ where } \mu_i \\ \text{are the eigenvalues of } A_q, \\ k_{q+1}\alpha_q N_q^* - m_q, \quad i = q+1, \\ -m_i, \quad i = q+2, \ldots, n. \end{cases}$$

Obviously, for $i = q+2, \ldots, n$ the condition $\lambda_i = -m_i < 0$ is satisfied. Since $N_q^* > 0$, for λ_{q+1} to be negative it is sufficient that

$$N_q^* < \frac{m_{q+1}}{\alpha_q k_{q+1}}. \tag{5.27}$$

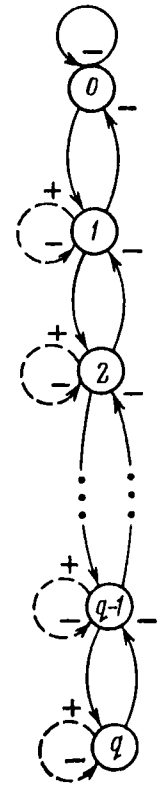

Fig. 34. SDG associated with matrix A_q. Broken lines correspond to $h_i > 0$ they vanish when $h_i = 0$.

If $q = n$, the condition (5.27) becomes unnecessary: when $\operatorname{Re} \mu_i < 0$ ($i = 0, \ldots, n$) a chain with n members is always stable.

Because all N_q^* ($i = 1, \ldots, q-1$) are positive when $N_q^* > 0$, b_i, d_i are positive as well. Hence, $\operatorname{Re} \mu_i < 0$, and if inequality (5.26)

is satisfied, the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ is asymptotically stable.

Using the explicit expression for N_q^* from (5.11) and (5.12), inequality (5.27) may be rewritten in the form

$$(1)\ Q < \alpha_0 f_{2S} f_{2S+1}, \qquad q = 2S; \tag{5.28}$$

$$(2)\ Q < \alpha_0 f_{2S+1} f_{2S+2}, \qquad q = 2S + 1, \tag{5.29}$$

or

$$Q < \alpha_0 f_q f_{q+1} = Q^* (q + 1). \tag{5.30}$$

Eventually, with regard to the above notation and the inequalities (5.13)-(5.14), *the necessary and sufficient condition for the open trophic chain with q members to exist is that the supply rate of the external resource be bounded from above and below*:

$$Q^* (q) < Q < Q^* (q + 1). \tag{5.31}$$

5.6. Conditions of existence of closed trophic chain of constant length

In this section we consider the problem of stability of the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$, but now in system (5.5). Linearizing in the neighborhood of the equilibrium, we get the matrix of the linearized system in the form somewhat different from (5.26):

$$F_1 = \begin{Vmatrix} A_q^1 & C \\ 0 & D_{n-q} \end{Vmatrix}. \tag{5.32}$$

Here

$$A_q^1 = \begin{Vmatrix} -b_0 & c_1 - d_0 & c_2 & \cdots & c_q \\ b_1 & & 0 & -d_1 & 0 \\ \vdots & \ddots & \vdots & \ddots & \vdots \\ 0 & b_{q-1} & 0 & & -d_{q-1} \\ & & b_{q-1} & & 0 \end{Vmatrix}, \qquad C = \begin{Vmatrix} c_{q+1} & c_{q+2} & \cdots & c_n \\ & 0 & & \end{Vmatrix},$$

$c_i = a_i m_i$, $i = 1, \ldots, n$, all the other notations being the same. As in the previous section, the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ is asymptotically stable, provided the inequality

$$N_q^* < \frac{m_{q+1}}{\alpha_q k_{q+1}} \tag{5.33}$$

is satisfied and the matrix A_q^1 (the submatrix of matrix (5.32) in the upper left corner) is stable. However A_q^1 does not belong to the class of Jacobian matrices, and we could not obtain sufficiently simple conditions which yield this matrix stability.

If a concrete value of q is pre-assigned, a recurrence relation for the characteristic polynomial $P_q(\lambda)$ of matrix A_q^1 somehow facili-

tates the check of appropriate relationships (say, for Hurwitz determinants):

$$P_q(\lambda) = -\lambda P_{q-1}(\lambda) + b_q d_{q-1} P_{q-2}(\lambda) - (-1)^q c_q b_1 \ldots b_q,$$
$$P_0(\lambda) = -\lambda - b_0, \tag{5.34}$$
$$P_1(\lambda) = \lambda^2 + b_0\lambda + b_1(d_0 - c_1).$$

It may be easily obtained when expanding the characteristic determinant of matrix A_q^1 in elements of the last row. If the characteristic equation $P_q(\lambda) = 0$ is written in the form

$$\lambda^{q+1} + e_q(q)\lambda^q + e_{q-1}(q)\lambda^{q-1} + \ldots + e_1(q)\lambda + e_0(q) = 0,$$

then using (5.34) one can write out the recurrence relations for coefficients $e_i(q)$:

$$e_i(q) = e_{i-1}(q-1) + b_q d_{q-1} e_i(q-2), \qquad i = 1, \ldots, q$$
$$e_{q+1}(q) = 1,$$
$$e_i(q) = 0, \; i = q+2, \ldots,$$
$$e_1(1) = b_0, \tag{5.35}$$
$$e_0(q) = b_q d_{q-1} e_0(q-2) - (-1)^q c_q b_1 \ldots b_q,$$
$$e_0(0) = b_0,$$
$$e_0(1) = b_1(d_0 - c_1).$$

Consider several particular cases. Put $q = 1$. Then matrix A_1^1 is stable, if $c_1 < d_0$ or $m_1 a_1 < \alpha_0 N_0^*$. And since $N_0^* = m_1/(\alpha_0 k_1)$, this condition takes the form $a_1 k_1 < 1$. In turn,

$$N_1^* = \frac{k_1 Q}{m_1(1 - a_1 k_1)} > 0,$$

only if $a_1 k_1 < 1$. Inequality (5.33) sets an upper bound to the supply rate of the resource

$$Q < \frac{m_1 m_2}{\alpha_1 k_1 k_2}(1 - a_1 k_1) = \tilde{Q}^*(2).$$

Thus, the restriction on the resource supply rate

$$\frac{m_1(1 - a_1 k_1)}{k_1} < Q < \frac{m_1 m_2}{\alpha_1 k_1 k_2}(1 - a_1 k_1)$$

is a necessary and sufficient condition for the existence of a stable equilibrium of the form $[N_0^*, N_1^*, 0, \ldots, 0]$, that is, for the existence of a 1-member trophic chain.

Let $q = 2$. Then matrix A_2^1 is stable, if $e_0(2), e_1(2), e_2(2) > 0$ and $e_1(2)\, e_2(2) > e_0(2)$, and using the expressions for $e_i(2)$ from (5.35), we get

$$b_0 d_1 > b_2 c_2, \qquad b_0(d_0 - c_1) + b_2 c_2 > 0.$$

The first inequality suggests that $a_2k_1k_2 < 1$, whereas the second one may be rewritten in the form

$$\alpha_0 N_0^* N_1^* - c_1 N_1^* + \frac{\alpha_2}{\alpha_0} c_2 N_2^* = Q + c_2 N_2^* \left(1 + \frac{\alpha_2}{\alpha_0}\right) > 0,$$

and is therefore satisfied for $N_2^* > 0$. But since

$$N_2^* = \frac{\alpha_1 k_1 k_2 Q - m_1 m_2 (1 - a_1 k_1)}{\alpha_1 m_2 (1 - a_2 k_1 k_2)} > 0$$

for $Q > \tilde{Q}^*$ (2), in this case again the stability of the steady state immediately follows from its existence.

To be biologically sensible, the products a_1k_1, $a_2k_1k_2$ cannot exceed unity. If a_1, a_2, k_1, $k_2 \to 1$, for the existence of steady states it is necessary that $Q \to 0$. The latter makes the system completely closed, with the total amount of resource in it remaining constant. However, this leads us to the singular case (one or several eigenvalues of matrix (5.32) become zero or pure imaginary), and we can say nothing about the steady state stability on the basis of linear approximation. The analysis of such systems will be the subject of Section 9.

Unfortunately, for $q > 2$ it is still unknown, whether the necessary conditions for the existence of an equilibrium of the type $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ are also sufficient for its stability. To answer this question, sufficient conditions for the stability of matrix A_q^1 are required. In principle, for every given q this problem is solvable (for instance, we can write down the appropriate Hurwitz determinants); however, reasoning along these lines we cannot derive constructive sufficient conditions. We are safe in saying that only for sufficiently small c_i matrix A_q^1 will be stable if matrix A_q is stable. In other words, when the closure plays a minor role ($a_i \ll 1$) the necessary conditions of existence of a closed trophic chain turn out to be sufficient.

Finally, we can formulate only the following statement (which is weaker than in Section 5): *if there exists a closed trophic chain with q members, the supply rate of the external resource should satisfy the restriction*

$$\tilde{Q}^*(q) < Q < \tilde{Q}^*(q+1), \tag{5.36}$$

where $\tilde{Q}^*(q)$ is given by formulas (5.23) and (5.24). By its sense $\tilde{Q}^*(q) > 0$, $q > 1$ and this requires that

$$\alpha_0 f_{2S-1} f_{2S} + \sigma_{2S} > f_{2S-1}\varphi_S + f_{2S}\psi_S, \qquad q = 2S,$$

$$\alpha_0 f_{2S} f_{2S+1} + \sigma_{2S+1} > f_{2S}\psi_{S+1} + f_{2S+1}\varphi_S, \qquad q = 2S + 1.$$

Simple but cumbersome calculations indicate that to satisfy these inequalities we need that

$$a_i k_1 k_2 \ldots k_i < 1, \qquad i = 1, \ldots, q. \tag{5.37}$$

Since by its sense $a_i \leqslant 1$, $k_i \leqslant 1$, we can say that in partially closed trophic chains the condition (5.37) is always met.

Let q be now an arbitrary integer. However suppose that $\sum_{i=1}^{n} a_i m_i N_i$ may be presented in the form

$$a_1 m_1 N_1 + \varepsilon \sum_{i=2}^{n} a_i m_i N_i,$$

where $\varepsilon > 0$ is small. Can this hypothesis be plausible? For real ecosystems it seems fairly justified. For instance, in land ecosystems the major part of dead organic matter is composed of dead foliage (fallen leaves of plants). Products of metabolism of animals and their carcases represent a very small fraction (<10%) of the total dead organic mass.

For $\varepsilon \to 0$,

$$\sum_{i=1}^{n} a_i m_i N_i \to a_1 m_1 N_1.$$

Therefore we should assume all c_i in the matrix (5.32) to be zero (except for $c_1 \neq 0$). Obviously, in this case matrix A_q^1 will again belong to the Jacobian class, and will be stable for $d_0 - c_1 > 0$. Thus, if the inequalities (5.33) and $c_1 < d_0$ are satisfied, there exists a trophic chain with q members (the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ is asymptotically stable).

Since in this case $c_i = 0$ $(i = 2, \ldots, q)$, in formulas for φ_s, ψ_S and σ_{2S} we should put $m_1 \neq 0$, $m_2, \ldots, m_q = 0$. Then $\varphi_S = \sigma_{2S} = \sigma_{2S+1} = 0$, $\psi_S = \psi_{S+1} = m_1 a_1$, and for $q = 2S$

$$\begin{aligned} N_0^* &= \frac{Q + m_1 a_1 f_{2S}}{\alpha_0 f_{2S}}, \qquad N_1^* = f_{2S}, \\ N_q^* &= N_{2S}^* = H_{2S-1}\left(\frac{Q + m_1 a_1 f_{2S}}{\alpha_0 f_{2S}} - f_{2S-1}\right), \end{aligned} \tag{5.38}$$

and for $q = 2S + 1$

$$\begin{aligned} N_0^* &= f_{2S+1}, \\ N_1^* &= \frac{Q}{\alpha_0 f_{2S+1} - a_1 m_1}, \\ N_q^* &= N_{2S+1}^* = H_{2S}'\left(\frac{Q}{\alpha_0 f_{2S+1} - a_1 m_1} - f_{2S}\right). \end{aligned} \tag{5.39}$$

Using the expressions for N_0^*, the inequality $c_1 < d_0$ may be rewritten in the form

$a_1 m_1 f_{2S} < Q + a_1 m_1 f_{2S}$, for even q,

$a_1 m_1 < \alpha_0 f_{2S+1}$, for odd q.

Obviously, for any $Q > 0$ the first inequality is satisfied. The second inequality is equivalent to

$$\alpha_0 f_{2S} f_{2S+1} - a_1 m_1 f_{2S} > 0.$$

As it follows from (5.24) for N_i^* ($i = 0, \ldots, q$) to be positive it is necessary that $Q > \alpha_0 f_{2S} f_{2S+1} - a_1 m_1 f_{2S}$ (for $c_1 \neq 0$, $c_i = 0$, $i = 2, \ldots, q$). Thus, the fact that N_i^* is positive provides that the inequality $c_1 < d_0$ is satisfied for odd q too. Therefore, the only inequality that remains is (5.32), which, if satisfied, assures stability of the equilibrium, i.e., a closed q-member trophic chain exists.

With the use of expressions for N_q^* from (5.38) and (5.39), the inequality (5.32) takes the form

$$Q < \alpha_0 f_{2S} f_{2S+1} - a_1 m_1 f_{2S}, \qquad q = 2S, \tag{5.40}$$

$$Q < \alpha_0 f_{2S+1} f_{2S+2} - a_1 m_1 f_{2S+2}, \quad q = 2S + 1. \tag{5.41}$$

And finally, *the necessary and sufficient condition of the existence of a q-member trophic chain closed only in the first level is that the supply rate of the external resource be bounded from above and below*:

$$\tilde{Q}^* (q) < Q < \tilde{Q}^* (q + 1). \qquad 5.42)$$

According to (5.23), (5.24) and (5.30), here we have

$$\tilde{Q}^* (q) = \alpha_0 f_{q-1} f_q - a_1 m_1 f_q = Q^* (q) - a_1 m_1 f_q \qquad (q \text{ is even})$$

$$\tilde{Q}^* (q) = \alpha_0 f_{q-1} f_q - a_1 m_1 f_{q-1} = Q^* (q) - a_1 m_1 f_{q-1} \qquad (q \text{ is odd}),$$

and $\tilde{Q}^* (1) = 0$.

Comparison between (5.42) and (5.31) shows, that a closed trophic chain may exist at lower supply rates of the external resource, than the open chain of the same length (this being quite natural, though).

5.7. Several case-studies and their interpretation

Consider a more simple situation, when parameters α_i, k_i, a_i and m_i are the same for all species. Then $\alpha_i = \alpha$, $k_i = g_i = k$, $a_i = a$, $m_i = m$ ($\mu_i = \mu$), and by formulas (5.9) and (5.10) we have

$$f_{2S-1} = f_{2S} = \frac{m}{\alpha k^S} \left(\frac{1 - k^S}{1 - k} \right),$$

$$f_{2S+1} = f_{2S+2} = \frac{m}{\alpha k^{S+1}} \left(\frac{1 - k^{S+1}}{1 - k} \right).$$

In this case the threshold rates $Q^* (q)$ and $\tilde{Q}^* (q)$ for the open and closed chains are, respectively,

(1) *Open chain*:

$$Q^*(q) = \frac{m^2}{\alpha k^q (1-k)^2}(1 - 2k^{q/2} + k^q) \qquad (\text{even } q)$$
$$Q^*(q) = \frac{m^2}{\alpha k^q (1-k)^2}(1 - (1+k)\, k^{(q-1)/2} + k^q) \qquad (\text{odd } q). \tag{5.43}$$

(2) *Closed chain*:

$$\tilde{Q}^*(q) = Q^*(q) - \frac{am^2}{\alpha k^{q/2}}\left(\frac{1-k^{q/2}}{1-k}\right) \qquad (\text{even } q)$$
$$\tilde{Q}^*(q) = \tilde{Q}^*(q) - \frac{am^2}{\alpha k^{(q-1)/2}}\left(\frac{1-k^{(q-1)/2}}{1-k}\right) \qquad (\text{odd } q). \tag{5.44}$$

Obviously, $k < 1$, and since the quantity $1 - k$ represents the fraction of biomass spent for respiration, metabolism, etc., in most real ecosystems k is sufficiently small. Therefore, instead of (5.43) and (5.44) one may use more simple approximations, derived from these relationships under the assumption of k being small. If we suppose that $am \sim O(1)$, then the estimates of $Q^*(q)$ to within $O(1/k^{(q-1)/2})$ are the same in open and closed chains; in this case they do not depend upon whether q is even or odd:

$$Q^*(q) \simeq \tilde{Q}^*(q) = \frac{m^2}{\alpha}\left(\frac{1}{k}\right)^q [1 + O(k)]. \tag{5.45}$$

Conditions (5.31) and (5.36) are then written in the form

$$\frac{m^2}{\alpha k^q} < Q < \frac{m^2}{\alpha k^{q+1}}. \tag{5.46}$$

Whence easily follows the estimate for the length of the trophic chain at a small k:

$$-\ln \frac{\alpha k Q}{m^2} \Big/ \ln k < q < -\ln \frac{\alpha Q}{m^2} \Big/ \ln k. \tag{5.47}$$

In the other extreme case, when $k \to 1$, the estimates are as follows

(1) *Open chain*:

$$Q^*(q) = \frac{m^2 q^2}{4\alpha} \qquad (\text{even } q)$$
$$Q^*(q) = \frac{m^2 (q^2 - 1)}{4\alpha} \qquad (\text{odd } q). \tag{5.48}$$

(2) *Closed chain*:

$$\tilde{Q}^*(q) = \frac{m^2}{4\alpha} q (q - 2a) \qquad (\text{even } q)$$
$$\tilde{Q}^*(q) = \frac{m^2}{4\alpha} (q-1)(q + 1 - 2a) \qquad (\text{odd } q). \tag{5.49}$$

It is peculiar that while for small k the estimates of threshold rates were the same for odd and even q, as $k \to 1$ the influence of

evenness begins to show up, and this effect may be neglected only at very high values of $q \gg 1$. In this case the estimate for q up to 0 (1) has the form:

(1) for an *open chain*

$$\sqrt{1+4\alpha Q/m^2}-1<q<2\sqrt{\alpha Q}/m; \tag{5.50}$$

(2) for a *closed chain*

$$a+\sqrt{(1-a)^2+4\alpha Q/m^2}-1<q<a+\sqrt{a^2+4\alpha Q/m^2}. \tag{5.51}$$

In order to compare how the trophic chain length grows with the resource supply rate at different values of k, the relationships between q and the dimensionless resource supply rate $\tilde{Q} = \alpha Q/m^2$ are

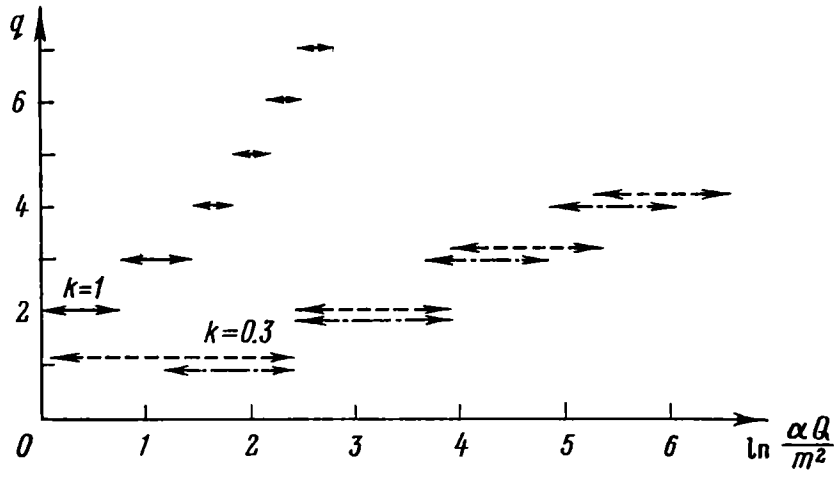

Fig. 35. Relationship between the trophic chain length and the supply rate of the external resource for different values of k (in the semi-log scale): ↔ $k = 1$; ← — → $k = 0.3$; ← · → $k = 0.3$—calculations by the approximate formula (5.47).

depicted in Fig. 35. Moreover, in Fig. 36 the length of the chain is shown for different values of k at a fixed value of $\bar{Q}$.

To illustrate the influence of the closure on the length of the trophic chain, and the relationship between the chain length q and the extent of closing of a, Fig. 37 displays variation of the threshold rates $\tilde{Q}^*$ (q) with a for several values of q (with $k = 1$), which separate the plane (Q, a) into domains of existence for chains with $q = 1, 2, \ldots$ members.

All these relationships are obviously interpreted well: the trophic chain length grows with k (the efficiency of transfer from one trophic level to another); with α, which can stand either for the energetic value of the biomass of a consumed species, or for its accessibility to the consumer; and with Q (the supply rate of the external resource).

When m (mortality coefficients) grow, the trophic chain length appropriately decreases. Closing the trophic chain, at a certain stage of recycling, will also result in chain elongation, but not more than by one member.

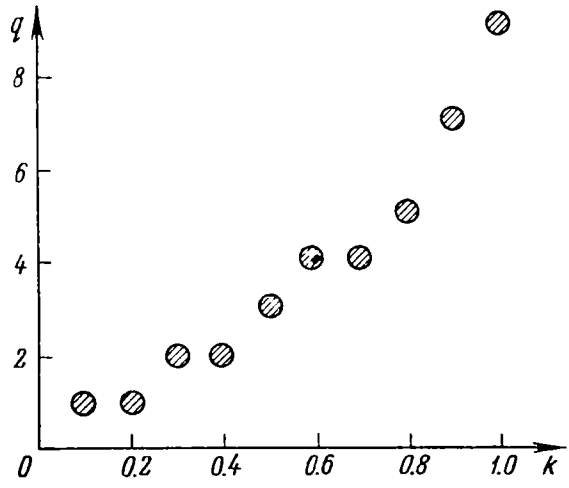

Fig. 36. Relationship between the trophic chain length and the variable k—the "average efficiency" of the ecosystem ($\alpha Q/m^2 = 20$).

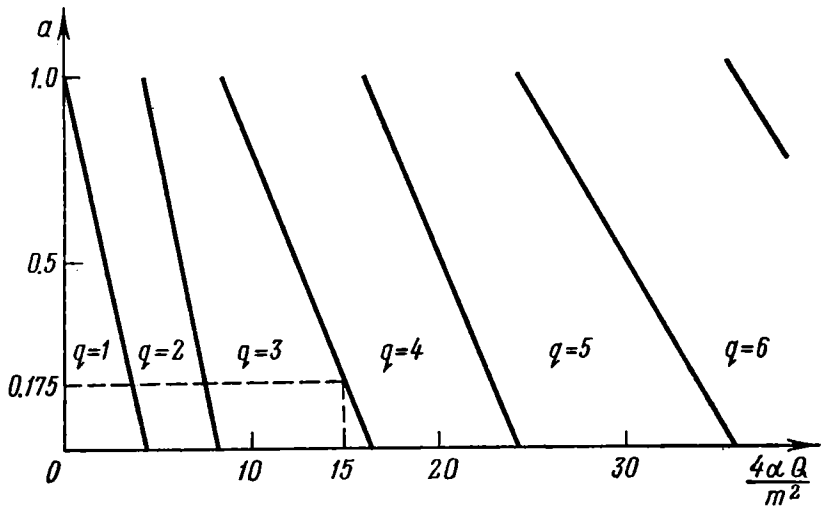

Fig. 37. Relationship between the threshold resource supply rates $\tilde{Q}^*$ (q) (in the form $4\alpha\tilde{Q}^*$ (q)$/m^2$) and the closure degree a. If, for instance, for $4\alpha Q/m^2 = 15$ the length of the open trophic chain is 3, then for the same supply rate of the external resource the length of the trophic chain with $a > 0.175$ is 4.

It is peculiar that the longer the trophic chain, the larger is the resource quantum, that should be supplied to the system for the introduction of a new species. In fact, according to (5.31) and (5.42), to increase the trophic chain length from q to $q + 1$ (introduction

of a new species into the system), the supply rate of the resource has to be increased by

$$h^0_{q,\,q+1} = \alpha_0 f_q (f_{q+1} - f_{q-1})$$

for an open chain, and by

$$h^1_{q,\,q+1} = h^0_{q,\,q+1} = \alpha_0 f_q (f_{q+1} - f_{q-1}) \qquad \text{(even } q\text{)}$$

$$h^1_{q,\,q+1} = (\alpha_0 f_q - a_1 m_1)(f_{q+1} - f_{q-1}) \qquad \text{(odd } q\text{)}$$

for a closed one. It is readily seen that $h^0_{q,q+1}$, $h^1_{q,q+1}$ are steadily growing functions of q. For instance, at small $k_i = k$ an estimate is valid:

$$h^0_{q,\,q+1} = h^1_{q,\,q+1} = \frac{m^2}{\alpha k^{q+1}} [1 + O(k)].$$

From all the foregoing it appears that the longer the trophic chain, the more effort it takes to introduce a new species (or a new trophic level) into the system. And the most interesting conclusion: *there are discrete levels of the external resource flow to the ecosystem, which determine the length of the trophic chain.* Stated another way, the energy supplied to the ecosystem is "quantified", the bigger the number of the possible new trophic level in the ecosystem, the larger energy "quantum" is to be supplied.

5.8. Generalization of trophic chain equations

Till now we considered the trophic chain equations, which were close to the Volterra ones. In doing so, the effects of "saturation" in trophic functions, existing in real nature (i.e. the fact that $V_i(N_i) \to \bar{V}_i < \infty$ when $N_i \to \infty$), and the competition effect in a trophic level were not taken into account. The latter may be accounted for, if a summand $\Gamma_i = -\gamma_i N_i^2$ $(i = 1, \ldots, q)$ is added to the right-hand sides of equations (5.1) and (5.2).

Clearly, the search for the state of equilibrium in this new system becomes much more complicated. Nevertheless, it is safe to say that all these states will be trophic chains, i.e. be of the form $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ $(q = 1, \ldots, n)$, and for each fixed q this state will be unique. We shall prove the uniqueness only for an open chain (for a closed one the proof is similar).

Steady-state equations have the form

$$\begin{aligned} &V_0^* N_1^* = Q, \\ &V_i^* N_{i+1}^* / N_i^* = k_i V_{i-1}^* - \gamma_i N_i^* - m_i, \qquad i = 1, \ldots, q-1 \\ &\gamma_q N_q^* = k_q V_{q-1}^* - m_q, \qquad V_i^* = V_i(N_i^*). \end{aligned} \tag{5.52}$$

Monotonicity of trophic functions implies that the equation $V_i(N_i) = p_i$ $(0 < p_i < V_i(\infty))$ has a sole solution N_i^*, therefore there

exists a one-to-one correspondence $p_i \xrightarrow{V_i} N_i^*$. Whence it immediately follows that if a value N_0^* is given, then $N_1^* = Q/V_0^*$ is defined uniquely.

Let $w_i = V_i^* N_{i+1}^*$. Then from (5.52) we get

$$w_i = k_i w_{i-1} - (m_i N_i^* + \gamma_i N_i^{*2}), \qquad w_0 = Q. \tag{5.53}$$

Considering this relationship a difference equation for w_i, we shall have

$$w_s = K_s Q - M_s, \tag{5.54}$$

where

$$K_s = k_1 k_2 \ldots k_s$$

$$M_s = m_s N_s^* + \gamma_s N_s^{*2} + k_s (m_{s-1} N_{s-1}^* + \gamma_{s-1} N_{s-1}^{*2}) + \ldots$$
$$\ldots + k_s k_{s-1} \ldots k_2 (m_1 N_1^* + \gamma_1 N_1^{*2}),$$

or

$$N_{s+1}^* = \frac{K_s Q - M_s (N_1^*, \ldots, N_s^*)}{V_s^* (N_s^*)}, \qquad N_1^* = \frac{Q}{V_0^*}. \tag{5.55}$$

Since we assume that all $N_i^* > 0$ $(i = 1, \ldots, q)$, for every N_0^* the relation (5.55) uniquely determines all the other N_i^*. In particular,

$$N_q^* = \frac{K_{q-1} Q - M_{q-1}}{V_{q-1}^*} = f_q (N_0^*). \tag{5.56}$$

On the other hand, from the last equation in (5.52) it follows that

$$\gamma_q N_q^{*2} = k_q V_{q-1}^* N_q^* - m_q N_q^*,$$

or

$$M_q = K_q Q, \quad \text{i.e.} \quad w_q = 0. \tag{5.57}$$

Considering this relationship an equation with respect to N_q^*:

$$\gamma_q N_q^{*2} + m_q N_q^* = K_q Q - k_q M_{q-1}, \tag{5.58}$$

we thus obtain an additional equation (besides (5.56)) for $N_q^* = f_q^1 (N_0^*)$, with $f_q \not\equiv f_q^1$. And this suggest that N_0^* cannot be chosen arbitrarily—it should be the solution to $f_q (N_0^*) = f_q^1 (N_0^*)$. To prove that this solution is unique, instead of the equation $f_q = f_q^1$ consider an equivalent equation (with respect to the variable N_q^*):

$$\gamma_q N_q^{*2} + m_q N_q^* = k_q V_{q-1}^* N_q^*, \tag{5.59}$$

which follows from (5.58), if we only notice that from (5.54)

$$K_q Q - k_q M_{q-1} = k_q w_{q-1} = k_q V_{q-1}^* N_q^*.$$

Obviously enough, (5.59) has a unique solution, and hence the equilibrium $[N_0^*, N_1^*, \ldots, N_q^*, 0, \ldots, 0]$ is also unique.

If $\gamma_q = 0$, instead of (5.58) we shall have

$$k_q V_{q-1}^* = m_q. \tag{5.60}$$

Relationship (5.60) uniquely defines the value of N_{q-1}^*, independently of the choice of N_0^*. Thus, by uniqueness of the mapping $N_{q-1}^* = f_{q-1}(N_0^*)$ given by (5.55), N_0^* may only be uniquely chosen. After $N_0^*, \ldots, N_{q-1}^*$ are calculated, the variable N_q^* is also defined uniquely [from (5.55)]. In consequence, in this case again the system may have only one trophic chain of a fixed length q.

Again, like before, the problem of the existence of a q-member trophic chain is reduced to stability analysis of a zero solution in a linearized system with a matrix of the form

$$\tilde{F} = \begin{Vmatrix} \tilde{A}_q & C \\ 0 & D_{n-q} \end{Vmatrix},$$

where

$$D_{n-q} = \operatorname{diag}\{-m_{q+1} + k_{q+1}V_q(N_q^*), -m_{q+2}, \ldots, -m_n\},$$

$$\tilde{A}_q = \begin{Vmatrix} -b_0 & c_1 - d_0 & c_2 & \ldots & c_q \\ b_1 & -h_1 & -d_1 & & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & b_{q-1} & -h_{q-1} & & -d_{q-1} \\ & & b_q & & -h_q \end{Vmatrix},$$

$$C = \begin{Vmatrix} c_{q+1} & \ldots & c_n \\ & 0 & \end{Vmatrix}.$$

Here we used

$$b_0 = N_1^* V_0'(N_0^*), \qquad b_i = k_i N_i^* V_{i-1}'(N_{i-1}^*),$$
$$d_0 = V_0(N_0^*), \qquad d_i = V_i(N_i^*),$$
$$h_i = \gamma_i N_i^* + N_{i+1}^*[V_i'(N_i^*) - V_i(N_i^*)/N_i^*],$$
$$c_i = a_i m_i, \qquad i = 1, \ldots, q.$$

$V_i'(N_i^*) > 0$ (for $N_i^* < \infty$) and all the b_i and d_i are positive, since the trophic functions steadily grow with N_i. For $k_{q+1}V_q(N_q^*) < m_{q+1}$ matrix $\tilde{F}$ is stable, provided that $\tilde{A}_q$ is stable. Otherwise $\tilde{F}$ is unstable.

If all c_i are zero, we deal with an open trophic chain. In this case $\tilde{A}_q = A_q$ is a Jacobian matrix and, as it has been shown in Section 5, for $h_i \geqslant 0$ it is stable.

How may the "saturation" effects and competition affect the trophic chain stability? The question is fairly simple to answer when the chain is open.

Let all γ_i be zero, so we have the pure saturation effect. Then $h_i = N_{i+1}[V_i'(N_i^*) - V_i^*/N_i^*]$. If the trophic function belongs to the first type (cf. Fig. 11), then $h_i < 0$ for all N_i^* and the trophic chains with these trophic functions are always unstable. If the trophic functions belong to type II or III, h_i will be negative only for sufficiently high values of N_i^*. As this takes place, matrix A_q (and $\tilde{F}$

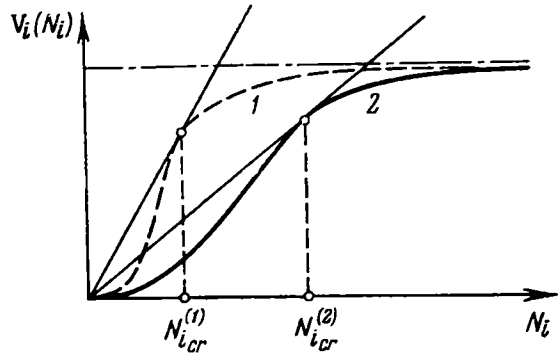

Fig. 38. Trophic functions with different settling rates of saturation (the 1st saturates faster than the 2nd). $N_{i\,cr}^{(1,2)}$ are the critical populations for the 1st and the 2nd functions, respectively. If $N_i^* < N_{i\,cr}$ then $h_i > 0$, but if $N_i^* > N_{i\,cr}$ then $h_i < 0$.

together with it) becomes unstable. It is peculiar that the earlier comes the saturation, the lower are the values N_i^*, for which the chain begins to break-up (cf. Fig. 38). Here stability is lost when at least one trophic level is saturated (it is sufficient for at least one h_i to become negative). That the trophic chain precisely breaks and does not change into a new state of equilibrium, being again a trophic chain of q members, follows from the proved uniqueness of a chain with a fixed number of species.

If $\gamma_i > 0$, a γ_i can always be found such that $h_i > 0$. Thus, competition within a trophic level stabilizes the system and makes for preservation of the chain.

5.9. Lyapunov functions and stability of trophic chain

To this point, while studying stability of equilibrium states in vertically structured ecosystems, we used the qualitative stability criterion. However, all the results (and even some more general ones) may be obtained, applying the direct Lyapunov method to systems linearized in the neighborhood of these states. We have shown above

that the stability problem for a trophic chain is reduced to stability analysis of matrix $\widetilde{A}_q$ or, which is the same, to stability analysis of a trivial solution to the system

$$\dot{\mathbf{x}}_q = \widetilde{A}_q x_q \qquad [(x_q)_i = N_i - N_i^*, \qquad i = 0, \ldots . q].$$

Before we proceed to set up Lyapunov functions, we introduce some notations. Let $\mathbf{x}$, $\mathbf{c}$, $\mathbf{b}$ be q-dimensional column vectors with the components $\mathbf{x} = [x_1, x_2, \ldots, x_q]^T$, $\mathbf{c} = [c_1 - d_0, c_2, \ldots, c_q]^T$, $\mathbf{b} = [b_1, 0, \ldots, 0]^T$, and B—a $q \times q$ matrix:

$$B = \begin{Vmatrix} -h_1 & -d_1 & & & \mathbf{0} \\ b_2 & -h_2 & -d_2 & & \\ & \ddots & \ddots & \ddots & \\ & b_{q-1} & -h_{q-1} & -d_{q-1} & \\ \mathbf{0} & & b_q & -h_q & \end{Vmatrix},$$

that is, a Jacobian matrix. For positive b_i and d_i and for $h_i \geqslant 0$ (say, $h_1 > 0$) it is stable. Then the system $\dot{\mathbf{x}}_q = \widetilde{A}_q \mathbf{x}_q$ may be written in the form

$$\frac{d\mathbf{x}}{dt} = B\mathbf{x} + x_0 b, \qquad \frac{dx_0}{dt} = \mathbf{c}^T\mathbf{x} - b_0 x_0. \tag{5.61}$$

Let all h_i be positive. We shall look for a Lyapunov function of the form

$$V(\mathbf{x}, x_0) = \mathbf{x}^T G \mathbf{x} + \frac{1}{2} x_0^2, \tag{5.62}$$

where $G = \operatorname{diag}\{g_1, \ldots, g_q\}$ $(g_i > 0)$. The total derivative of this function along the trajectories of system (5.61) is expressed by

$$-\frac{dV}{dt} = \mathbf{x}^T F \mathbf{x} + 2\mathbf{l}^T \mathbf{x} x_0 + b_0 x_0^2, \tag{5.63}$$

where vector $\mathbf{l}$ has the form

$$\mathbf{l} = -G\mathbf{b} - \frac{1}{2}\mathbf{c} \tag{5.64}$$

and matrix F satisfies the relationship

$$B^T G + GB = -F. \tag{5.65}$$

The last equation represents the well-known Lyapunov's matrix relationship, which for a stable matrix B should be satisfied by some positive definite matrices G and F. Since matrix B and the form of matrix G are already defined, equation (5.65) should have

a unique solution, given by elements

$$f_{ij}=\begin{cases} 2h_ig_i, & i=j=1,\ \ldots,\ q,\\ -b_ig_i+d_{i-1}g_{i-1}, & i=2,\ \ldots,\ q,\quad j=i-1,\\ -b_{i+1}g_{i+1}+d_ig_i, & i=1,\ \ldots,\ q-1,\quad j=i+1,\\ 0,\ |i-j|\geqslant 2. \end{cases}$$

Require that $f_{ij}=f_{ji}=0$ for $i\neq j$. Then

$$g_i=g_{i-1}\frac{d_{i-1}}{b_i}=g_1\frac{d_1d_2\ \ldots\ d_{i-1}}{b_2b_3\ \ldots\ b_i}=g_1\tilde{g}_i,\qquad i=2,\ \ldots,\ q, \tag{5.66}$$

and if $b_i>0$, $h_i>0$, then F is a diagonal matrix with positive elements, that is, F is positive definite.

Using the concrete form of G and $\mathbf{c}$ from (5.64), we get

$$l_1=-g_1b_1+\frac{1}{2}(d_0-c_1)=-g_1b_1+\frac{1}{2}\tilde{d}_0, \tag{5.67}$$

$$l_i=-\frac{1}{2}c_i,\qquad i=2,\ \ldots,\ q.$$

Separating the complete squares in the expression for dV/dt we will have

$$-\frac{dV}{dt}(\mathbf{x}^T+x_0\mathbf{l}^TF^{-1})\,F\,(\mathbf{x}+x_0F^{-1}\mathbf{l})+(b_0-\mathbf{l}^TF^{-1}\mathbf{l})\,x_0^2.$$

Hence on account of F being positive definite, the sufficient condition for dV/dt to be negative definite follows immediately:

$$b_0>\mathbf{l}^TF^{-1}\mathbf{l}=\sum_{i=1}^{q}\frac{l_i^2}{2h_ig_1\tilde{g}_i}\qquad(\tilde{g}_1=1). \tag{5.68}$$

$V(\mathbf{x},x_0)=0$ only at the point $[0,0]$ and $V\to\infty$ as $x_0^2+x_1^2+\ldots+x_q^2\to\infty$. Therefore, if there exists a $g_1>0$ such that the inequality (5.68) holds, then the function $V(\mathbf{x},x_0)$ is a Lyapunov function for system (5.61), i.e. the solution $[\mathbf{x}=\mathbf{0},\ x_0=0]$ to this system is stable. Naturally, matrix $\tilde{A}_q$ is then stable, too.

Show that such g_1 exists. Inequality (5.68) may be rewritten as

$$b_1^2g_1^2-(2b_0h_1+\tilde{d}_0b_1)\,g_1+\frac{1}{4}(\tilde{d}_0^2+\Phi^2)<0, \tag{5.69}$$

where

$$\Phi^2=\sum_{i=2}^{q}\frac{h_1}{h_i\tilde{g}_i}c_i^2.$$

It is sufficient to find a minimum to this square trinomial and require that it be attained at $(g_1)_{\min} > 0$ and be negative. Since

$$(g_1)_{\min} = \frac{2b_0h_1 + \tilde{d}_0 b_1}{2b_1^2} \quad \cdot \ (\tilde{d}_0 = d_0 - c_1),$$

for $2b_0h_1 > -\tilde{d}_0 b_1$ this value is positive. Substituting $(g_1)_{\min}$ into (5.69), we get the sufficient stability condition in the following form:

$$b_0 [b_1 (d_0 - c_1) + b_0 h_1] > \frac{b_1^2}{4} \sum_{i=2}^{q} \frac{c_i^2}{h_i \tilde{g}_i}. \tag{5.70}$$

It is readily seen that when (5.70) is satisfied, inequality $2b_0h_1 > > -\tilde{d}_0 b_1$ always holds and $(g_1)_{\min} > 0$.

If the trophic functions linearly depend upon the populations $[V_i (N_i) = \alpha_i N_i]$, then (5.70) becomes

$$N_1^* \left[(\alpha_0 N_0^* - a_1 m_1) + \frac{\gamma_1}{k_1} \right] > \sum_{i=2}^{q} \frac{K_i N_i^* a_i m_i}{4\gamma_i}, \tag{5.71}$$

where $K_i = k_1 k_2 \ldots k_i$. Functions K_i decline very rapidly with i, since in real ecosystems k_i are very small. If also the extent of recycling is low ($a_i m_i \ll 1$), and the intraspecific competition is strong enough, the chain will be stable for sure. (Naturally, the sufficient stability condition $k_{q+1} V_q^* < m_{q+1}$ is to be met.) Apparently, the chain stability may be also ensured if the biomass on the first trophic level by far exceeds the biomasses on all the other levels.

Suppose now $c_1 \neq 0$, $c_2 = \ldots = c_q = 0$, $h_1 = \ldots = h_q = 0$. Here condition (5.70) gives no answer to the question of stability. However, returning to expression (5.63) for dV/dt we see that

$$-\frac{dV}{dt} = \left(\frac{1}{2} \tilde{d}_0 - g_1 b_1 \right) x_0 x_1 + b_0 x_0^2.$$

The choice of $g_1 = \tilde{d}_0/(2b_1)$ makes dV/dt negative definite. But then (for $\tilde{d}_0 = d_0 - c_1 > 0$) the form $\mathbf{x}^T G \mathbf{x}$ is no longer sign definite, but is only sign-constant. In this case still $V(\mathbf{x}, x_0)$ is a Lyapunov function, whereas the solution $[\mathbf{x} = \mathbf{0}, x_0 = 0]$ is asymptotically stable. This follows from the Barbashin-Krasovsky theorem* about asymptotic stability on the whole. It states that for asymptotic stability it is sufficient that the manifold M, for which $dV/dt = 0$ ($dV/dt < 0$ outside M), have no entire system trajectories. In our case this manifold coincides with the hyperplane $\{\mathbf{x} \neq \mathbf{0}, x_0 = 0\}$. If $x_i(t) \neq 0$, $i = 1, \ldots, q$, $x_0(t) = 0$, then $\dot{x}_0 = -(b_0 - c_1) x_1$ and any trajectory leaves this plane. Similarly for $x_0 = x_1 = 0$, $x_i \neq 0$, $i = 2, \ldots, q$, $\dot{x}_1 = -d_1 x_2$, etc., till $x_0 = x_1 = \ldots =$

* Barbashin E. A., *Introduction to stability theory*, Nauka, Moscow, 1967, pp. 46-47 (in Russian). We use this theorem for a linearized system, and for linear systems local asymptotic stability is equivalent to stability on the whole.

$= x_{q-2} = 0$. The last two equations take the form $\dot{x}_{q-1} = -d_{q-1}x_q$, $\dot{x}_q = b_q x_{q-1}$. For $x_{q-1} = 0$, $x_q = \text{const}$, but this constant should be zero, for else the trajectory leaves the manifold $\{x_0 = x_1 = \ldots \ldots = x_{q-1} = 0,\ x_q = \text{const} \neq 0\}$. Accordingly, manifold M contains no entire trajectories, moreover $x_0 \equiv x_1 \equiv \ldots \equiv x_q \equiv 0$, and all the theorem conditions are satisfied. Thus in another way we get the result, already proved in Section 6.

Unfortunately, the Lyapunov function of the form (5.62) gives no answer to the stability problem in the case where some c_i differ from zero ($i \geqslant 2$) or if some h_i (or all of them) are zero.

5.10. Branching trophic chains

When studying real ecosystems it often occurs that in some trophic level the chain begins to branch and further on we have two (or even more) different chains (Fig. 39). What can be said about stability of such structures?

Let the chain branch, say, in two (or maybe more—this restriction is not important) on the sth level. The chain originating directly from the external resource will be considered *principal* (it has q members), and the other one (with r members, originating from the branching point)—*lateral*. And let the system parameters be such that there exists a nontrivial equilibrium of the form $[N_0^*, N_1^*, \ldots \ldots, N_q^*;\ N_1'^*, \ldots, N_r'^*]$. And we suppose that the conditions of the type $k_{q+1}V_q^* < m_{q+1}$ and $k'_{r+1}V_r'^* < m'_{r+1}$ are always met. These conditions bound from above the lengths of both chains.

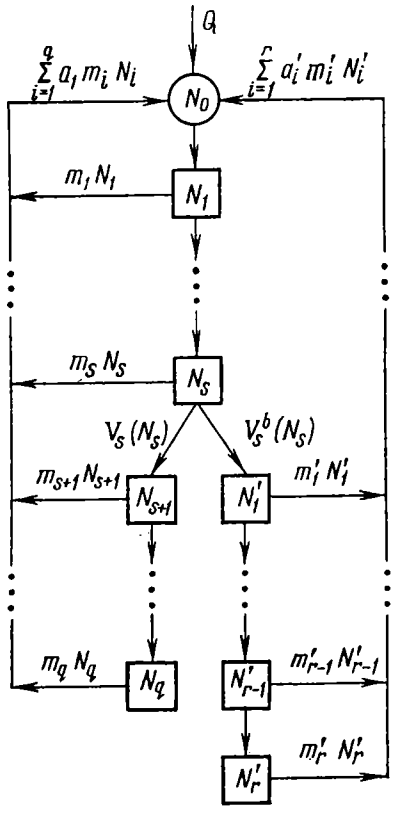

Fig. 39. Diagram of a branching trophic chain: $N_0 \to N_1 \to \ldots \to N_s \to N_{s+1} \to \ldots \to N_q$ is the principal chain; $N'_1 \to \ldots \to N'_{r-1} \to N'_r$ is the lateral chain.

The equations, linearized in the neighborhood of the equilibrium state, may be written in the form:

$$\begin{aligned} \frac{d\mathbf{x}}{dt} &= B\mathbf{x} + b_1 x_0 \boldsymbol{\delta}_1 - d_s^b x_1' \boldsymbol{\delta}_s, \\ \frac{d\mathbf{x}'}{dt} &= B'\mathbf{x}' + b_1' x_s \boldsymbol{\delta}_1, \\ \frac{d\mathbf{x}_0}{dt} &= \mathbf{c}^T\mathbf{x} + \mathbf{c}'^T\mathbf{x}' - b_0 x_0, \end{aligned} \tag{5.72}$$

where B and B' are Jacobian $q \times q$ and $r \times r$ matrices of the same type as in Section 5.9, δ_j is a column vector with zeros in all positions except the jth, where there is a 1, $\mathbf{c}' = [c_1', c_2', \ldots, c_r']$. Vector $\mathbf{x}'$ components are the population displacements from their equilibria in the lateral chain; $d_s^b = N_s^* V_s^b (N_s^*)$, where $V_s^b (N_s)$ is the trophic function for species in the 1st level of the lateral chain, depending upon the population (or biomass) in the sth level of the principal chain:

$$b_1' = k_1' N_1'^* \, dV_s^b (N_s^*)/dN_s.$$

The Lyapunov function will again be sought for in the form

$$V(\mathbf{x}, \mathbf{x}', x_0) = \mathbf{x}^T G \mathbf{x} + \mathbf{x}'^T G' \mathbf{x}' + \frac{1}{2} x_0^2, \tag{5.73}$$

where G, G' are diagonal matrices with elements g_i, $g_k' > 0$ ($i = 1, \ldots, q$; $k = 1, \ldots, r$). Calculating the derivative for this function we obtain

$$-\frac{dV}{dt} = \mathbf{x}^T F \mathbf{x} + \mathbf{x}'^T F' \mathbf{x} + 2x_0 (\mathbf{l}^T \mathbf{x} + \mathbf{l}'^T x') + d_s^b x_1' (\delta_s^T G \mathbf{x}) - b_1' x_s (\delta_1^T G' \mathbf{x}') + b_0 x_0^2, \tag{5.74}$$

where

$$\mathbf{l} = -c_1 \mathbf{e} - \frac{1}{2} \mathbf{c}, \qquad \mathbf{l}' = -\frac{1}{2} \mathbf{c}',$$

and G, F, B and G', F', B' must satisfy Lyapunov's matrix equation. If we now assume (as in Section 5.9) that

$$g_i = g_{i-1} \frac{d_{i-1}}{b_i}, \qquad g_k' = g_{k-1}' \frac{d_{k-1}'}{b_k'}, \tag{5.75}$$

where g_1 and g_1' are arbitrary positive numbers, then F and as F' are to be positive diagonal matrices. Choose g_1' such that

$$d_s^b x_1' (\delta_s^T G \mathbf{x}) = b_1' x_s (\delta_1^T G' \mathbf{x}'),$$

or

$$g_1' = g_s \frac{d_s^b}{b_1'} = g_1 \frac{d_1 d_2 \ldots d_{s-1} d_s^b}{b_1' b_2 \ldots b_s} = g_1 \Lambda_s. \tag{5.76}$$

Then using a method similar to that in Section 5.9, $-dV/dt$ is reduced to a sum of squares, and the sufficient condition for dV/dt to be

negative definite is that the inequality

$$b_0 > \mathbf{l}^T F^{-1} \mathbf{l} + \mathbf{l}'^T F'^{-1} \mathbf{l}' \tag{5.77}$$

be satisfied.

Further, using the arguments of Section 5.9, we get the sufficient condition for stability of a branching trophic chain in the form

$$b_0 \left[b_1 (d_0 - c_1) + b_0 h_1\right] > \frac{b_1^2}{4} \left(\sum_{i=2}^{q} \frac{c_i^2}{h_i \tilde{g}_i} + \sum_{k=1}^{r} \frac{c_k'^2}{h_k' \tilde{g}_k'} \right), \tag{5.78}$$

where

$$\tilde{g}_i = \frac{d_1 \ldots d_{i-1}}{b_2 \ldots b_i}, \qquad \tilde{g}_k' = \Lambda_s \frac{d_1' \ldots d_k'}{b_2' \ldots b_k'}.$$

While the left-hand side of the inequality has no relation to parameters of the lateral chain, the right-hand side increases when the branch appears. This can be given the following interpretation: chain branching makes the stability domain smaller and thus reduces the whole system stability. However, if the lateral chain is open, i.e. $c_k' = 0$ ($k = 1, \ldots, r$), then branching does not affect stability of the chain.

Finally, if all c_i, c_k', h_i and h_k' equal zero (except for maybe c_1, but in this case it is sufficient that $d_0 > c_1$), then the branching chain is always stable (the equilibrium state is asymptotically stable). The proof uses the same arguments as for the non-branching chain.

5.11. Some properties of closed systems

So far we considered ecosystems (with open or closed chains), with the resource cycle, which was not closed completely. There is, however, a whole class of artificial ecosystems where matter is completely recycled—these are the biological life-supporting systems of spaceships. A lot of natural ecosystems are also almost closed for some nutrients (say, nitrogen or phosphorus). Therefore it would be interesting to study some properties of such ecosystems.

A complete closure indicates that the substance conservation law is satisfied in the system, that is,

$$R(t) + \sum_{i=1}^{n} N_i(t) \equiv M = \text{const}. \tag{5.79}$$

System (5.2) will have an integral of the form (5.79) only if $Q = 0$ and $k_i = a_i = 1$, $i = 1, \ldots, n$. In this case, using (5.79) and assuming that the trophic functions are linear, instead of (5.2) for

model equations we shall have

$$\frac{dN_1}{dt} = N_1\left(\beta - \alpha_0 \sum_{i=1}^{n} N_i - \alpha_1 N_2\right), \qquad \beta = \alpha_0 M - m_1,$$

$$\frac{dN_i}{dt} = N_i(-m_i + \alpha_{i-1}N_{i-1} - \alpha_i N_{i+1}), \qquad i = 2, \ldots, n, \tag{5.80}$$

$$N_{n+1} = 0.$$

This system has a set of equilibria $[N_1^*, N_2^*, \ldots, N_q^*, 0, \ldots, 0]$ $(q = 1, \ldots, n)$, and the state $[N_1^*, 0, \ldots, 0]$ is always stable when $M > m_1/\alpha_0$. When $M < m_1/\alpha_0$ the only stable state will be the trivial one (with zero populations of all species), thus corresponding to complete ecosystem extinction.

With the methods, already used in Sections 5.3 and 5.4, one may obtain inequalities for parameters, which provide existence of a positive stationary solution, that is, of positive N_i^* $(i = 1, \ldots, q)$:

$$M > f_{2S-1}(1 + \varphi_S^0) + f_{2S}\psi_S^0 - \sigma_{2S}^0 = M^*(q), \qquad q = 2S, \tag{5.81}$$

$$M > f_{2S}\psi_{S+1}^0 + f_{2S+1}(1 + \varphi_S^0) - \sigma_{2S+1}^0 = M^*(q), \tag{5.82}$$

$$q = 2S + 1.$$

Here f_{2S-1}, f_{2S} are defined as in Section 5.3 (but for $k_i \equiv 1$), and φ_S^0, ψ_S^0, ψ_{S+1}^0, σ_{2S}^0, σ_{2S+1}^0 coincide with the functions φ_S, ψ_S, ψ_{S+1}, σ_{2S}, σ_{2S+1} introduced in Section 5.4 and taken here for $a_i m_i \equiv 1$.

Examine now the equations of the linear approximation. The matrix has the same structure as in Section 5.6, however, with lower dimensions: $q \times q$ instead of $(q + 1) \times (q + 1)$. In this case $c_i = -\alpha_0 N_1^* = -b_1$ $(i = 1, \ldots, n)$ and

$$A_q^1 = \begin{Vmatrix} -b_1 & -(b_1 + d_1) & -b_1 & & & -b_1 \\ b_2 & 0 & -d_2 & & & \\ & \cdot & \cdot & \cdot & & \\ & & \cdot & \cdot & \cdot & \\ & & & \cdot & \cdot & \cdot \\ 0 & & & b_{q-1} & 0 & -d_{q-1} \\ & & & & b_q & 0 \end{Vmatrix}, \tag{5.83}$$

where $b_i = \alpha_{i-1}N_1^*$, $d_i = \alpha_i N_i^*$ $(i = 1, \ldots, q)$. As in Sections 5.5 and 5.6, for a q-member trophic chain to be stable $(q \leqslant n)$, the inequality

$$N_q^* < m_{q+1}/\alpha_q \tag{5.84}$$

should be necessarily satisfied. From the recurrence relation for the characteristic polynomial of A_q^1:

$$F_q(\lambda) = -\lambda F_{q-1}(\lambda) + b_q d_{q-1} F_{q-2}(\lambda) + (-1)^q b_1 \ldots b_q,$$
$$F_2(\lambda) = \lambda^2 + b_1\lambda + (b_1 + d_1) b_2,$$
$$F_1(\lambda) = -\lambda - b_1,$$

it follows that all its coefficients have the same sign. This necessary stability condition is far from being sufficient when $q > 2$. For instance $q = 3$ requires another inequality $\alpha_0 + \alpha_1 > \alpha_2$ to be satisfied. For greater q the conditions become even more complicated.

Returning to inequality (5.84), on rearranging we can write

$$M < M^*(q + 1), \tag{5.85}$$

where $M^*(q + 1)$ is given by (5.81) and (5.82). Inequalities (5.81), (5.82) and (5.85) bound from above and below the total amount of resource M in the system, which is necessary for a completely closed q-member trophic chain to exist:

$$M^*(q) < M < M^*(q + 1). \tag{5.86}$$

However, when $q > 2$ this condition does not ensure asymptotic stability of the trophic chain.

Consider a particular case, when $\alpha_0 = \alpha_i = \alpha$, $m_i = m$ for all $i = 1, \ldots, n$. This may be possible, if we assume that the relative amount of prey (and the resource), consumed by the next level predator is the same for all levels, and, what is more, all species mortalities are equal. Then

$$\begin{gathered}
f_{2S-1} = f_{2S} = \frac{m}{\alpha} S, \\
\varphi_S^0 = \psi_S^0 = S, \\
\sigma_{2S} = \frac{m}{\alpha} S^2, \qquad \sigma_{2S+1} = \frac{m}{\alpha} S(S+1); \\
M^*(q) = \frac{m}{4\alpha} q(q+2), \qquad q = 2S, \\
M^*(q) = \frac{m}{4\alpha} (q+1)^2, \qquad q = 2S+1.
\end{gathered} \tag{5.87}$$

Whence immediately follows the estimate of the possible chain length (number of trophic levels) in a closed ecosystem at a given total amount of biomass (or total initial resource). For instance, when M is large enough ($\alpha M/m \gg 1$),

$$q \simeq 2\sqrt{\alpha M/m}. \tag{5.88}$$

5.12. Some properties of solutions to trophic chain equations

Solutions to original non-linear equations of models (5.4) and (5.5) exhibit several important properties. First of all we shall prove the following:

1. *If a system has a non-trivial equilibrium* $[N_0^*, N_1^*, \ldots, N_n^*]$, *then any system trajectory, initiating inside the positive orthant* P, *stays there.*

2. *No system trajectory tends to infinity.*

If we now prove that any steady state with one or several zero components N_s^* $(s \ll n)$ is unstable, then, according to the specific form of equations (5.4) and (5.5), this immediately implies that a trajectory with positive initial values leads inside the orthant P^n.

Consider an open chain with n levels. Let the system have a non-trivial equilibrium $[N_0^*, N_1^*, \ldots, N_n^*]$, thus requiring, as shown in Section 5.3, that

$$Q > \alpha_0 f_{n-1} f_n. \tag{5.89}$$

Along with this equilibrium, the system may have a steady state of the form $[\tilde{N}_0^*, \tilde{N}_1^*, \ldots, \tilde{N}_{n-1}^*, 0]$, which can easily be shown to be unstable for $\tilde{N}_{n-1}^* > m_n/(\alpha_{n-1} k_n)$. Using (5.11) and (5.12) the last inequality may be rearranged to get

$$H_{n-2}\left(\frac{Q}{\alpha_0 f_{n-1}} - f_{n-2}\right) - \frac{\mu_n}{g_n} > 0, \tag{5.90}$$

where either $n = 2S + 1$ or $n = 2S$. On substituting (5.89) into (5.90) we get

$$\frac{Q}{\alpha_0 f_{n-1}} - f_{n-2} - \frac{\mu_n}{g_n H_{n-2}} > f_n - f_{n-2} - \frac{\mu_n}{g_n H_{n-2}} = 0,$$

that is, if (5.89) is satisfied, then (5.90) also holds.

Instability of other steady states with zero populations is proved in much the same way, as well as instability of such equilibria in a closed chain.

Consequently, if a system has a non-trivial steady state, then any system trajectory, initiating inside the positive orthant, stays there. This conclusion is also valid for chains of length $q < n$, only in this case the orthant has less dimensions.

The second statement is proved by induction in q. For $q = 1$ system (5.5) takes the form

$$\begin{aligned} \frac{dN_0}{dt} &= Q - \alpha_0 N_0 N_1 + a_1 m_1 N_1, \\ \frac{dN_1}{dt} &= N_1(-m_1 + k_1 \alpha_0 N_0). \end{aligned} \tag{5.91}$$

In the positive quadrant this system has only one equilibrium which can easily be shown to be locally asymptotically stable.

If on the phase plane there were trajectories leading to infinity, they would be separated from trajectories tending to $[N_0^*, N_1^*]$ by a separatrix. This separatrix should either initiate in a singular point of the system, or be a limit cycle. The first alternative does not work, since there is only one singular point, that is the stable equilibrium (5.91) $[N_0^*, N_1^*]$, whereas the absence of closed trajectories in the system readily follows from the Dulack criterion (used already in Section 3.5). Thus for $q = 1$ the statement is proved.

Suppose the statement is valid for any $q = l + 1$ and prove that it holds for $q = l + 2$ as well. The two last equations in system (5.5) in this case take the form

$$\begin{aligned} \frac{dN_{l+1}}{dt} &= N_{l+1}(-m_{l+1} + k_{l+1}\alpha_l N_l - \alpha_{l+1}N_{l+2}), \\ \frac{dN_{l+2}}{dt} &= N_{l+2}(-m_{l+2} + k_{l+2}\alpha_{l+1}N_{l+1}). \end{aligned} \tag{5.92}$$

Since N_l is bounded above, i.e. $N_l \leqslant C_l < \infty$ in place of (5.92) one may write

$$\begin{aligned} \frac{dN_{l+1}}{dt} &\leqslant N_{l+1}(-m_{l+1} + k_{l+1}\alpha_1 C_l - \alpha_{l+1}N_{l+2}), \\ \frac{dN_{l+2}}{dt} &= N_{l+2}(-m_{l+2} + k_{l+2}\alpha_{l+1}N_{l+1}). \end{aligned} \tag{5.93}$$

Consider the extreme case, where there is an equality sign in (5.93). In this case we obtain the classical Volterra predator-prey system with no self-limitation, the solutions to which are always bounded. The more so will be the solutions to (5.92) for any finite N_l, and hence the solutions to the entire system (5.93) for $q = l + 2$. Our statement is proved.

Finally, any solution to system (5.5) is bounded, and there is not a single trajectory leading to infinity.

Likewise, it is proved that the solutions to (5.80) are positive for positive initial values and the total amount of resource restricted by (5.81), (5.82) (i.e. the case of a completely closed chain with $a_i K_i = 1$). The solutions boundedness follows immediately from the existence of integral (5.79).

Accordingly, if there exists a non-trivial equilibrium of a q-member-trophic-chain type ($q \leqslant n$), the solutions of model equations are always positive and bounded (provided that the initial values $\mathbf{N}(0) \in P^q$). Obviously, only $k_i \leqslant 1$ and $a_i \leqslant 1$ are biologically meaningful, that is, $a_i K_i \leqslant 1$.

Consider now the variables

$$\mathcal{N}_i(t) = \frac{1}{t}\int_0^t N_i(\tau)\,d\tau,$$

which are the average N_i values over the interval $(0, t)$. Multiplying each equation in (5.5) by a quantity $1/K_i$ $(K_i = k_1 \ldots k_i)$ and adding them up term by term, we get

$$\sum_{i=0}^{n} \frac{1}{K_i}\frac{dN_i}{dt} = Q - \sum_{i=1}^{n} R_i N_i, \qquad R_i = \frac{m_i(1-a_iK_i)}{K_i}, \tag{5.94}$$

or on integrating

$$\frac{1}{t}\sum_{i=0}^{n} \frac{N_i - N_i(0)}{K_i} = Q - \sum_{i=1}^{n} R_i \mathcal{N}_i. \tag{5.95}$$

Integrating (5.5) term by term with respect to t, for $i = 1, \ldots, n$, we get

$$\frac{1}{t}\ln\frac{N_i(t)}{N_i(0)} = -m_i + k_i\alpha_{i-1}\mathcal{N}_{i-1} - \alpha_i\mathcal{N}_{i+1}, \qquad i = 1, \ldots, n. \tag{5.96}$$

System (5.95)-(5.96) is a linear algebraic system with respect to the variables $\mathcal{N}_i$ $(i = 0, 1, \ldots, n)$. For $t \to \infty$ it coincides with the steady-state equations, since $N_i(t)$ are bounded. Hence when $t \to \infty$ $\mathcal{N}_i(t)$ have limits N_i^*, i.e. *asymptotic means of species populations and the resource amounts equal their steady-state values.*

If system (5.5) has periodic solutions (cycles) with a period T, then, since $N_i(t+T) = N_i(t)$, in complete analogy we derive similar conclusions about cyclic means

$$N_i^c = \frac{1}{T}\int_t^{t+T} N_i(\tau)\,d\tau.$$

In the case of a completely closed chain the appropriate conclusions are immediately attained from equations (5.80). In fact, integrating them with respect to t and then dividing through by t, we see that as $t \to \infty$ the equations obtained for asymptotic means coincide with the steady-state equations. If periodic solutions are assumed to exist, then similar equations are derived for cyclic means.

The last equation in system (5.5) implies that

$$N_n(t) = N_n(0)\exp\left\{-m_n t + k_n\alpha_{n-1}\int_0^t N_{n-1}(\tau)\,d\tau\right\}. \tag{5.97}$$

Obviously, if for $t \to \infty$

$$\frac{m_n}{k_n \alpha_{n-1}} > \frac{1}{t} \int_0^t N_{n-1}(\tau)\, d\tau, \tag{5.98}$$

then $N_n(t) \to 0$, i.e. any trajectory originating from P^n approaches P^{n-1}. But since $\mathcal{N}_{n-1} \to N^*_{n-1}$, the condition (5.98) is equivalent to the condition

$$\frac{m_n}{k_n \alpha_{n-1}} > N^*_{n-1}. \tag{5.99}$$

If we now assume that $n = q + 1$, then the condition (5.99) bounds above the resource supply rate Q (or the total resource M), whereas the requirement that all N_i^* $(i = 1, \ldots, q)$ be positive gives the appropriate lower bounds.

Finally, if the supply rate of the external resource Q (total resource M) is bounded by (5.31) for an open chain, or by (5.36) for a closed one, or lastly, by (5.86) for a completely closed chain, then for any initial displacements, provided that they do not bring one or several species to complete extinction, and for any t the first q species populations remain bounded (both above and below), i.e. these species may exist infinitely long. The populations of the following species: $(q + 1)$ th, . . ., nth,—approach zero as $t \to \infty$, i.e. these species are eliminated from the system.

In this case we can speak about *ecological stability* of a q-member trophic chain.

5.13. Ecological stability of trophic chains

Evidently, the requirement of ecological stability is less restricting than simply stability in Lyapunov's sense (just as for the requirement of solutions boundedness, termed often *stability in Lagrange's sense*). As it was noted above, to consider an ecosystem stable it is sufficient that the comprising species coexist indefinitely, with their populations neither growing to infinity, nor declining to zero. A trophic chain satisfies all these conditions when the resource supply rate or its total amount are bounded by some quantities.

On the other hand, these restrictions define the length of the chain. Therefore, if the chain length is already settled, then one may say that this chain will be always ecologically stable. Thus, the necessary existence conditions for trophic chain of a certain length are necessary and sufficient for the chain ecological stability. (A similar feature has been already mentioned for conservative and dissipative communities in Section 4.3 where the requirement of Lyapunov stability for the equilibrium $\mathbf{N}^*$ turned out to be not only necessary, but also sufficient for ecological stability.)

Thus, if the characteristics of the chain comprising species (levels) are given: the trophic functions, efficiencies of resource processing, natural mortality coefficients—then using formulas (5.31), (5.36) and (5.86) one may derive the upper and lower limits for the resource supply rate (total amount of resource), and thereby for each fixed rate (fixed amount of resource) define the length of the trophic chain, the latter being always ecologically stable.

And in conclusion it should be noted, that though almost all the above speculations were related to chains with linear trophic functions and with no intraspecific (intralevel) competition, the main deductions seem to hold for chains characterized by generalized equations too.

5.14. Silver-Springs ecosystem

To verify our theory of trophic chains we will make use of experimental evidence provided by H. Odum in his thorough study of the concrete ecosystem of warm Silver-Springs in Florida.

It is very important for this ecological community to maintain a stable steady state, while all the variations of biomass are of seasonal origin. Odum presents data on the standing crops and energy flows for five trophic levels: producers (N_1), herbivores (N_2), carnivores (N_3), higher predators (N_4) and decomposers that close the trophic chains. The biomass on these levels (in g of dry weight/m^2) equals respectively: $N_1^* = 809$, $N_2^* = 37$, $N_3^* = 11$, $N_4^* = 1.5$; the decomposer biomass equals 5. Energy will be treated as the deciding resource, therefore the chain may be considered open. For the same reason the decomposers, feeding on dead organic matter and thus closing the chain for substances, are not included in our chain. It should be noted, however, that the trophic chain equations (5.4) admit accumulation of unutilized resource, whereas solar energy in its original form, obviously, cannot be accumulated. Nevertheless, these equations may find application here, since at equilibrium all the incoming resource is immediately taken up by the first trophic level, flowing through the block R with no losses. On the other hand, as we shall see below, the threshold rates Q^* (q) we are interested in, depend neither upon N_0^*, nor upon α_0, i.e. values governing the state of the resource variable. The diagram of energy flows in the ecosystem is illustrated in Fig. 40, where all the quantities are in kcal/m^2. The diagram is somewhat simplified as compared with the original one of H. Odum. In particular, mortality (the m_iN_i terms) covers not only the fraction of biomass-enclosed energy, which goes to decomposers, but also the biomass energy carried from the system with the flow. Moreover, the flow of organic matter from outside is neglected (since its value is relatively small).

Using formulas of Section 5.3, we shall calculate the threshold rates $Q^*(q)$:

$$
\begin{aligned}
Q^*(2) &= \frac{m_1 m_2}{\alpha_1 k_1 k_2}, \\
Q^*(3) &= Q^*(2)\left(1 + \frac{\alpha_1 m_3}{\alpha_2 m_1 k_3}\right), \\
Q^*(4) &= Q^*(3)\left(1 + \frac{\alpha_2 m_4}{\alpha_3 m_2 k_4}\right), \\
Q^*(5) &= Q^*(4)\left(1 + \frac{\alpha_1 \alpha_3 m_5}{\alpha_4 k_5 (\alpha_2 k_3 m_1 + \alpha_1 m_3)}\right).
\end{aligned}
\tag{5.100}
$$

From these relations one may see that $Q^*(q)$ do not depend upon α_0.

$k_1 = 0.42$, since $\alpha_a N_0^* N_1^* = Q = 20810$ and $k_1 \alpha_a N_0^* N_1^* = 8833$. Likewise $k_2 = 0.44$, $k_3 = 0.175$, $k_4 = 0.286$. The steady-state biomasses of the levels are in grams of dry weight, while the energy flows are in kilocalories; therefore suppose that the scaling coefficient is r, so that $N_1^* = 809r$ (kcal/m^2), and so on. Particular values of r are unessential for us, since m_i and α_i appear in the expressions for $Q^*(q)$ in combinations such that the coefficients r may be mutually cancelled.

$m_1 = 6.755/r$, $m_2 = 29.6/r$, $m_3 = 4.18/r$, $m_4 = 4/r$,

since

$m_1 N_1^* = 5465$, $m_2 N_2^* = 1095$,

$m_3 N_3^* = 46$, $m_4 N_4^* = 6$.

From equalities

$\alpha_1 N_1^* N_2^* = 3368$, $\alpha_2 N_2^* N_3^* = 383$,

$\alpha_3 N_3^* N_4^* = 21$

it respectively follows that

$\alpha_1 = 0.1125/r^2$, $\alpha_2 = 0.956/r^2$,

$\alpha_3 = 1.27/r^2$.

Substituting for m_i and α_i in (14.1) we get

$Q^*(2) = 9585$, $Q^*(3) = 13\,611$,

$Q^*(4) = 18\,456$.

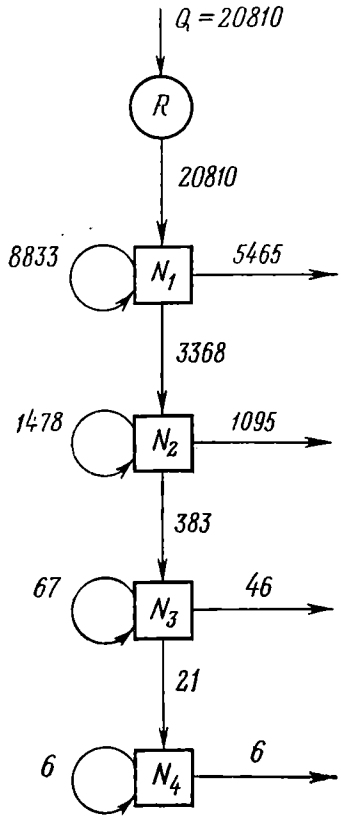

Fig. 40. A simplified diagram of energy flows in the ecosystem of Silver-Springs.

It is apparent, that the real resource supply rate Q is higher than $Q^*(4)$, that is, the productivity of the producers level and the ecosystem parameters are such that four trophic levels may exist. Suppose we want to introduce into the fifth level of the ecosystem

a species that preys upon specimens of the fourth level. Let this species have the same characteristics as those of the fourth level species, that is $k_5 = k_4$, $m_5 = m_4$ and $\alpha_4 = \alpha_3$. Then according to (5.100) Q^* (5) = 36 613, i.e. for successful introduction the resource supply rate Q (or the productivity of the first level) should necessarily be almost doubled. On the other hand, if the producer productivity for some reasons (say, toxic pollution) decreases only by 12%, then the stability of the non-trivial equilibrium with four levels will be disturbed, and hence the higher predators will be eliminated.

Consider now an averaged ecosystem with parameters $k_i = k = 0.3$, $\alpha_i = \alpha = 0.8/r^2$ and a mean mortality coefficient $m_i = m$, which takes on several values: $5/r$, $7.5/r$, and $11/r$. The values of the dimensionless variable $\ln(\alpha Q/m^2)$ are then 6.5, 5.69, and 4.92, respectively, and from the graph in Fig. 35 one may see, that the ecosystem will comprise 4, 4, and 3 levels, respectively. This again indicates, that even in rich ecosystems, such as Silver Springs, the number of trophic levels is small. In ecosystems of higher latitudes, the number of levels may be even smaller, since respiration expenditures of organisms increase there and the efficiency of biomass processing lessens. The influence of this effect may be reduced by a further straining of trophic links, which results in a decrease in the fraction of dying biomass; however, this decrease is made up for by a general deterioration of environmental conditions. In consequence the probability of specimen death increases. To find the total impact of these two conflicting effects, additional investigations are required, including those based on the models of this chapter.

5.15. Notes and bibliography

To 5.1. It has repeatedly been attempted to deduce an aggregate dynamic characteristic of an ecosystem with several trophic levels. For instance, in the paper:

Alexeev A. A., Krishev I. I., "Kinetic equations to describe ecosystem dynamics," *Biophysics*, 19, 4, pp. 754-759, 1974, (in Russian)

dynamic equations for averaged biomasses on two trophic levels are derived using methods of statistical mechanics. It was supposed that ecological characteristics of species on each trophic level were sufficiently close. A somewhat different treatment is given in:

Tansky M., "Structure, stability and efficiency of ecosystem," In: "*Progress in theoretical biology*," Eds. R. Rosen, F. M. Snell, Acad. Press, N.Y., pp. 206-262, 1976,

where all the species in each trophic level were taken to be the same, however, species populations on levels were taken as new dynamic variables. To find their equilibria it was postulated, that in a stable-steady state the ratio P/B (productivity to total ecosystem biomass) should be minimal. As a result, structures were obtained much like real trophic pyramids of ecosystems.

To 5.2. Equations (5.4) for an open trophic chain are very close to the Volterra ones, differing only in the equation for the resource. Modifications of this

kind for classical Volterra equations were applied, for instance, by V. A. Kostitzin in describing global biochemical cycles:

Kostitzin V. A., "*L'évolution de l'atmosphère*,": Hermann, P., 1935.

Equations of the form (5.5) (for $Q \equiv 0$) were derived in the paper:

Eman (Bulgakova) T. I., "On some mathematical ecosystem models", Nauka, Moscow, pp. 191-202, 1966 ("*Problems of cybernetics*," Vol. 16),

where these equations described a biogeocenosis. A community with an "inert" component was thought of as a biogeocenosis; respectively, a classical Volterra model was used to account for this biogeocenosis. It was proved that a biogeocenosis may have a non-trivial equilibrium for any number of species (and not only for an even number as the Volterra model), and under certain conditions it will be stable. Besides, other modifications of Volterra models were suggested in this work. The major distinction of these models from those considered in this chapter is that an equilibrium of only one type has been investigated; in other words, the trophic chain length has been supposed to be fixed.

To 5.3. The existence of "paradoxical" trophic chains was first disclosed when studying eutrophicating lakes. It turns out that for an enhanced nutrient enrichment (pollution by domestic waste waters, leaching of fertilizers from neighboring fields), ordinary trophic chains may become paradoxical (see, for instance,

Loucks O. L. et al., "Studies of Lake Wingra watershed," Univ. of Wisconsin, Madison, 1977).

To 5.5. The work by:

Schwartz H. R., "Ein Verfahren zur Stabilitatsfrage von Matrizen-Eigenwert-Problem," *Z. Angew. Math. Phys.*, **7**, 3, S. 473-500, 1956,

is concerned with stability analysis of Jacobian matrices. The stability conditions, stated in this work, immediately suggest, for instance, that matrix (4.32) is stable.

To 5.9. The method used here to construct the Lyapunov function, is due to A. I. Loorye, who worked on stability in some systems of automatic control:

Loorye A. I., *Some non-linear problems in automatic control theory*, Gostechizdat, Moscow, 1951 (in Russian).

However, instead of the original formulation, we used Loorye's method as presented in the book:

Lefschetz S., *Stability of nonlinear control systems*, N.Y., 1965.

To 5.10. A number of interesting problems for branching trophic chains were considered in:

Alexseev V. V., "Biogeocenosis—autogenerators and triggers," *Journal of General Biology*, **37**, 6, pp. 738-744, 1976 (in Russian)

where ecosystem dynamics was analyzed for two trophic levels with two species in each and with a possibility for branching (existence of crossed trophic links). Curiously enough, this system may generate both self-oscillations and oscillations of the trigger type.

To 5.14. All the experimental evidence utilized in this section are taken from the work:

Odum H. T., "Trophic structure and productivity of Silver Springs, Florida," *Ecol. Monogr.*, **27**, pp. 55-112, 1957.

CHAPTER 6

ECOLOGICAL NICHE OVERLAP AND STABILITY OF HORIZONTALLY STRUCTURED COMMUNITIES

6.1. Ecological introduction

While in the previous chapter vertically structured communities, with interactions between trophic levels, were considered, the present chapter is concerned with interactions between species in a trophic level, or, in other words, in horizontally structured communities. Of the five theoretically possible types of interaction between species in one level (cf. Section 4.1) we shall only consider competition, since, on the one hand, this is the most widespread type in nature, and on the other, the mathematical theory of communities with competition is better developed by far than models of symbiosis, amensalism, or commensalism.

Organisms of any biological species are characterized by a certain range of physical and ecological conditions, in which they survive and multiply with success. From this naturally follows the concept of the so-called *ecological niche*—a domain in the space of vitally important environmental factors (for example, specific composition and size of food, site conditions, etc.), within which the species existence is ensured and beyond which this existence is impossible or next to impossible. Despite this concept being intuitively clear, the definition of an ecological niche gives rise to a number of difficulties, and at present this question cannot find a unified interpretation in the literature. However the undeniable point that each species occupies its ecological niche invites the question: "Can niches of several different species overlap?" Observations indicate that ecological niche overlap is typical of real communities. Species may coexist not only being in similar physical and geographical conditions, but also consuming the same resources. That resources are limited imposes natural restrictions on total populations of species, rely on the former, so that the growth of species population with a common resource is mutually restricted. Thus ecological niche overlap naturally results in relations of competition, and the ecological niche naturally determines the place and role of a given species in the structure of a competitive community.

Since competitive communities cannot be qualitatively stable (cf. Section 4.6), the problem presents itself of determining stability

domains for parameters of a competition model, or rather of determining the structure of niche overlap, which provides stable coexistence of competitors, the so-called *species packing*.

The ecological niche concept is closely related to the well-known *competitive exclusion principle* of G. F. Gause, which forbids coexistence of two species with similar ecological requirements in one and the same habitat. It is the limits to niche overlap in a stable community that point to the limits to ecological similarity of species that persist together. Species packing analysis thus enables us to obtain theoretical conditions for elimination of particular species from the competitive community, as well as conditions under which some species may successfully invade the community.

The study of these problems using mathematical models is primarily based upon a formal definition of an ecological niche, by which the chapter is opened.

6.2. Formalization of niche notion and dynamic equations for competition

In the literature several different definitions of the ecological niche can be found. From the mathematician's viewpoint, the most appropriate among them is the one that, while presenting the essence, lends itself to formalising. A successful compromise of this kind is the niche definition based upon the notions of a *resource spectrum* and a *utilization function*.

Suppose the resource consumed by biological species is characterized by some parameter x (size of the uptaken food, its specific composition, space coordinates of the habitat, etc.), which is multivariate in the general case; and suppose the amount of resource characterized by x, which is available for consumption, is determined by a function K (x). Then the set of values x with the function K (x) defined on it is called a *resource spectrum* (or *space*).

Moreover, let the resource consumed by a given species be described by some probability density distribution f (x), which is the *utilization function*, with the mean x_0 and a finite variance σ^2. Then the *ecological niche* is defined by the point x_0 on the resource spectrum and the function f (x)—the density of the random distribution around x_0. For example, organisms of some species most willingly uptake food of size x_0, the consumption of food of other sizes is governed by some theoretical or empirical probability rule with the density f (x). The preferred size x_0 is naturally viewed as the *centre of the niche*, and the root-mean-square deviation σ as the *niche breadth*, characterizing to what extent the given species is specialized in uptaking resource x: small σ values suggest high specialization, large σ low specialization.

Clearly, increasing the dimensionality of vector x, one may attain theoretically complete adequacy of the introduced definition to the living conditions of a biological species. However, to make the quantitative analysis of models clearer and simpler, in our further treatment we assumed that resource spectrum is one-dimensional. In most cases the results obtained can be generalized in a natural and simple way.

When we look at communities with several species, competing for common resources, the points x_0, which belong to different species, are naturally thought of as (and this is in accord with observations)

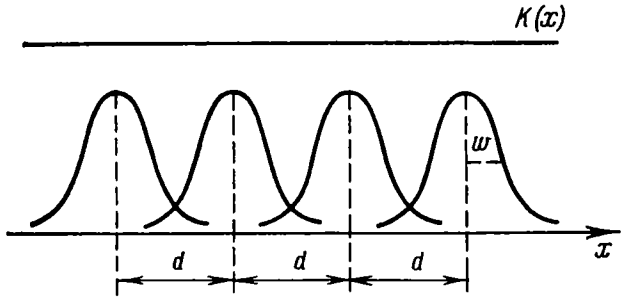

Fig. 41. One-dimensional resource spectrum $K(x)$ and the overlap of ecological niches determined by normal utilization functions.

separated by finite distances. In this case, the competition phenomenon itself, connected with the overlap of ecological niches for competing species, appears within the adopted formalism as a result of intersecting domains of definition for the appropriate utilization functions $f_i(x)$ in the resource space. The most simple (idealized) example of the kind is illustrated in Fig. 41, where $f_i(x)$ are presented by similar curves of a normal distribution uniformly spaced along the resource spectrum with the separation d between mean values; $K(x) \equiv$ const. If w is a mean square deviation common for all the curves, then the ratio w/d may be considered a measure of closeness of niches, or a measure of how closely species are packed, and by stability conditions one may judge about the tolerable limits of niche overlap.

In the dynamic model of an n-species competitive community, the populations $N_i(t)$ will be expressed in units of the uptaken resource. In doing so, the product $f_i(x) N_i(t)$ assumes the sense of the fraction of the overall resource consumed by the ith species, which is uptaken at point x of the resource spectrum. Then

$$K(x) - \sum_{i=1}^{n} f_i(x) N_i(t)$$

is nothing but the local (on resource spectrum) difference between potentially available and actually necessary amount of resource for $[N_1(t), \ldots, N_n(t)]$ to coexist. As far as the resource does not limit the species population growth (for small populations) the population may be thought of to grow exponentially with the intrinsic natural birth rate coefficient r_i:

$$\frac{d(f_i(x) N_i)}{dt} = r_i f_i(x) N_i, \qquad i = 1, \ldots, n. \tag{6.1}$$

The limiting effect of competition may be expressed by the relative measure of resource depletion at point x:

$$[K(x) - \sum_{i=1}^{n} f_i(x) N_i(t)]/K(x), \tag{6.2}$$

whereupon the ith species dynamics at point x of its ecological niche is given by the equation

$$f_i(x) \frac{dN_i}{dt} = \frac{r_i N_i}{K(x)} f_i(x) \left[K(x) - \sum_{j=1}^{n} f_j(x) N_j\right]. \tag{6.3}$$

Integrating (6.3) throughout the resource spectrum yields

$$K_i \frac{dN_i}{dt} = r_i N_i \left(K_i - \sum_{j=1}^{n} \alpha_{ij} N_j\right), \qquad i = 1, \ldots, n, \tag{6.4}$$

where

$$K_i = \int K(x) f_i(x)\, dx \tag{6.5}$$

presents the total amount of resource consumed by the ith species—the so-called *niche capacity*. The *coefficient of competition* between ith and jth species

$$\alpha_{ij} = \int f_i(x) f_j(x)\, dx, \tag{6.6}$$

is in proportion to the total probability (throughout the spectrum) that the consumer interests for the given pair of species meet at one and the same point on the spectrum, and thus characterizes the degree of their niche overlap.

Deviding through (6.4) by K_i, we get a system of equations

$$\frac{dN_i}{dt} = r_i N_i - \frac{r_i}{K_i} \sum_{j=1}^{n} \alpha_{ij} N_i N_j, \qquad i = 1, \ldots, n, \tag{6.7}$$

which is coincident up to notations with the general type Volterra system [cf. (4.2)]. Notice that the scaling substitution of variables

$\widetilde{N}_i = K_i N_i / r_i$ brings (6.7) to the form

$$\frac{d\widetilde{N}_i}{dt} = r_i \widetilde{N}_i - \sum_{j=1}^{n} \gamma_{ij} \widetilde{N}_i \widetilde{N}_j, \tag{6.8}$$

where

$$\gamma_{ij} = \alpha_{ij} \frac{r_i r_j}{K_i K_j}, \tag{6.9}$$

so that matrix $\| \gamma_{ij} \|$ retains the symmetry property of matrix $A = \| \alpha_{ij} \|$.

System (6.7) is dissipative in the sense of V. Volterra, since

$$F(\mathbf{y}) = \sum_{i,j=1}^{n} \alpha_{ij} y_i y_j = \int \sum_{i,j} f_i(x) y_i f_j(x) y_j \, dx$$

$$= \int \left[\sum_{i=1}^{n} f_i(x) y_i \right]^2 dx > 0$$

for all $\mathbf{y} \neq 0$, i.e. the quadratic form is positive definite. Dissipativity implies that if (6.7) has a positive stationary solution, then it must be asymptotically stable throughout the positive orthant P^n, and, what is more, this equilibrium stability turns out to be not only a sufficient condition for a stable operation of an n-species competitive community, but a necessary one as well. Therefore, a stability criterion for a competitive community is given by existence conditions of a positive equilibrium, that is a positive solution to a linear system

$$A\mathbf{N} = \mathbf{K}, \qquad \mathbf{K} = [K_1, \ldots, K_n] > 0. \tag{6.10}$$

Below, in Section 6.4, we shall give a "geometric" interpretation for positiveness of solutions to (6.10), and meanwhile consider a community of competing species with Gaussian utilization functions. For each species

$$f_i(x) = (2\pi w_i^2)^{-1/2} \exp\left\{ \frac{-(x - x_i)^2}{2w_i^2} \right\}, \tag{6.11}$$

where x_i is the mean value or the niche centre, and w_i^2 is the variance of the normal distribution. If the niche centres for the ith and jth species are separated by d_{ij}, then

$$\alpha_{ij} = \frac{1}{2\pi w_i w_j} \int_{-\infty}^{\infty} \exp\left\{ -\frac{x^2}{2w_i^2} - \frac{(x - d_{ij})^2}{2w_j^2} \right\} dx$$

$$= \frac{1}{\sqrt{2\pi (w_i^2 + w_j^2)}} \exp\left\{ -\frac{d_{ij}^2}{2(w_i^2 + w_j^2)} \right\}. \tag{6.12}$$

If all $f_i(x)$ have a common variance $w_i^2 = w^2$ and the niches are labeled sequentially, then $d_{ij} = |i - j| d$ and

$$\alpha_{ij} = \frac{1}{2w\sqrt{\pi}} \exp\left\{-\frac{(i-j)^2 d^2}{4w^2}\right\}. \tag{6.13}$$

The normalization of competition coefficients α_{ij} in a way such, that the degree of niche overlap equals unity, gives

$$\alpha_{ij} = a^{(i-j)^2}, \qquad a = \exp\{-d^2/4w^2\}; \tag{6.14}$$

and the corresponding competition matrix has the form

$$A = \begin{Vmatrix} 1 & a & a^4 & \dots & a^{(n-1)^2} \\ a & 1 & a & \dots & \\ a^4 & a & 1 & \dots & \\ \dots & \dots & \dots & \dots & \dots \\ a^{(n-1)^2} & & \dots & & 1 \end{Vmatrix}. \tag{6.15}$$

Dissipativity of matrix (6.15), resulting from the integral representation (6.6) of the competition coefficients, is thus preserved for all values of the ratio d/w that is a measure of how closely the species are packed in the community. Hence, formally for an arbitrary close packing (small d/w) the equilibrium $\mathbf{N}^*$ will be stable. However it may be shown, that for $n \gg 1$ the smallest eigenvalue of A, which specifies how fast the perturbed trajectory equilibrates, is

$$\lambda_{\min} \approx 1 - 2a + 2a^4 - 2a^9 + 2a^{16} - \dots,$$

which gives for small d/w

$$\lambda_{\min} \approx 4\sqrt{\pi}\frac{w}{d}\exp\{-\pi^2 w^2/d^2\}. \tag{6.16}$$

It follows that for substantial niche overlap, i.e. for $d/w \to 0$, although $\lambda_{\min}$ is still positive, formally providing equilibrium asymptotic stability, it tends to zero faster than any finite power of d/w, thus having an essential singularity at zero. This results in extremely long damping times for the perturbed trajectory.

Besides, direct computer runs for different n within the range of $n = 100$ indicate that for small d/w, that is for a sufficiently close to 1, negative numbers occur among the components of the solution of (6.10) (when the right-hand sides are the same). This implies that in order to preserve stability an increase in niche overlap necessarily requires that the function $K(x)$ be changed in a specific way, such that the set of niche capacities keep the solutions of (6.10) positive. More details may be found below.

6.3. Another representation of competition coefficients

If utilization functions for all species in the competitive community are known, the calculation of competition coefficients presents no principle difficulties. However, in practice the exact form of $f_i(x)$

is generally unknown, and occasionally when the limiting resource is essentially multivariate, the form possibly cannot be specified for sure. Therefore, it would be of interest to study the properties of system (6.7) with no reference to the integral representation (6.6) for the competition coefficients α_{ij}.

Suppose n species are labeled in such a way that their number difference $| i - j |$ may be used as a measure of their niches separation on the resource continuum. It is only natural to assume that competition decreases as niches are separated, i.e. formally

$$\alpha_{ij} = \alpha (| i - j |), \tag{6.17}$$

where $\alpha (z) > 0$ is a decreasing function of an integral argument. Notice that (6.14) is a special case of this relationship for

$$\alpha (z) = a^{z^2}.$$

Thus, the farther the species are separated from one another, the less their ecological niches overlap.

Thus, the object of our further analysis is a symmetric matrix A with positive elements, whose values only depend upon the difference of the row and column numbers. Recall that in the case of a symmetric matrix the properties of stability, D-stability, total stability, and dissipativity are equivalent (Section 4.5), so that for system (6.7) with competition coefficients (6.17) to be dissipative, it is sufficient that A spectrum is positive. Examples prove that the above restrictions on the structure of A are still insufficient to answer the question of whether or not there exists a positive stable equilibrium $\mathbf{N}^*$.

The structure given by (6.17) enables us to establish one intuitively evident property of the solution to the steady-state system of equations (6.10), namely that solutions are symmetric about the "centre", when the right-hand side vector exhibits this property.

Theorem 1. Let $A = \| \alpha_{ij} \|$ *be an* $n \times n$*-matrix with elements* $\alpha_{ij} = \alpha (| i - j |)$, *where* $\alpha (z)$ *is a function of integral argument, such that det* $\| \alpha_{ij} \| \neq 0$; let vector $\mathbf{K} = [K_1, \ldots, K_n]$ *be symmetric, i.e.* $K_i = K_{n-i}$. *Then the solution to the system of linear equations* $A\mathbf{x} = \mathbf{K}$ *is also symmetric, i.e.* $x_i = x_{n-i}$.

Proof. For definiteness, we consider the case of $n = 6$ (for an arbitrary n the pattern of the proof is the same). With no loss of generality, we assume that

$$\alpha (0) = 1, \qquad \alpha (1) = \alpha, \qquad \alpha (2) = \beta,$$

$$\alpha (3) = \gamma, \qquad \alpha (4) = \delta, \qquad \alpha (5) = \varepsilon.$$

As a result, the system of equations will take the form

$$\begin{Vmatrix} 1 & \alpha & \beta & \gamma & \delta & \varepsilon \\ \alpha & 1 & \alpha & \beta & \gamma & \delta \\ \beta & \alpha & 1 & \alpha & \beta & \gamma \\ \gamma & \beta & \alpha & 1 & \alpha & \beta \\ \delta & \gamma & \beta & \alpha & 1 & \alpha \\ \varepsilon & \delta & \gamma & \beta & \alpha & 1 \end{Vmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \\ x_6 \end{bmatrix} = \begin{bmatrix} K_1 \\ K_2 \\ K_3 \\ K_4 \\ K_5 \\ K_6 \end{bmatrix}. \tag{6.18}$$

Now we rearrange (6.18) in the following way: subtract the last equation from the first one, the last but one equation from the second one, and so on. We get

$$\begin{Vmatrix} 1-\varepsilon & \alpha-\delta & \beta-\gamma & \gamma-\beta & \delta-\alpha & \varepsilon-1 \\ \alpha-\delta & 1-\gamma & \alpha-\beta & \beta-\alpha & \gamma-1 & \delta-\alpha \\ \beta-\gamma & \alpha-\beta & 1-\alpha & \alpha-1 & \beta-\alpha & \gamma-\beta \\ \gamma & \beta & \alpha & 1 & \alpha & \beta \\ \delta & \gamma & \beta & \alpha & 1 & \alpha \\ \varepsilon & \delta & \gamma & \beta & \alpha & 1 \end{Vmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \\ x_6 \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \\ K_4 \\ K_5 \\ K_6 \end{bmatrix}. \tag{6.19}$$

In the first three equations of (6.19) group together the variables x_1 and x_6, x_2 and x_5, x_3 and x_4 to yield

$$\begin{Vmatrix} 1-\varepsilon & \alpha-\delta & \beta-\gamma \\ \alpha-\delta & 1-\gamma & \alpha-\beta \\ \beta-\gamma & \alpha-\beta & 1-\alpha \end{Vmatrix} \begin{vmatrix} x_1-x_6 \\ x_2-x_5 \\ x_3-x_4 \end{vmatrix} = 0. \tag{6.20}$$

If the determinant for (6.20) $D' \neq 0$, its only solution is zero, that is $x_1 = x_6$, $x_2 = x_5$, $x_3 = x_4$, exactly what the theorem states. To prove that $D' \neq 0$, notice, that when we switch from (6.18) to (6.19), the determinant D of (6.18) remains unchanged, and a further equivalent rearrangement of its columns gives

$$D = \begin{vmatrix} 1-\varepsilon & \alpha-\delta & \beta-\gamma & 0 & 0 & 0 \\ \alpha-\delta & 1-\gamma & \alpha-\beta & 0 & 0 & 0 \\ \beta-\gamma & \alpha-\beta & 1-\alpha & 0 & 0 & 0 \\ \gamma & \beta & \alpha & 1+\alpha & \alpha+\beta & \beta+\gamma \\ \delta & \gamma & \beta & \alpha+\beta & 1+\gamma & \alpha+\delta \\ \varepsilon & \delta & \gamma & \beta+\gamma & \alpha+\delta & 1+\varepsilon \end{vmatrix}$$

$$= D' \begin{vmatrix} 1+\alpha & \alpha+\beta & \beta+\gamma \\ \alpha+\beta & 1+\gamma & \alpha+\delta \\ \beta+\gamma & \alpha+\delta & 1+\varepsilon \end{vmatrix}.$$

As stated, $D \neq 0$ and hence $D' \neq 0$, thus proving the theorem. For an odd n the treatment is similar but for the only difference that the unpaired component of the solution $x_{(n+1)/2}$ takes no part in system (6.20). But at any value of $x_{(n+1)/2}$ symmetry of x is preserved.

Consider some special cases of relationship (6.17). Suppose each of n species only competes with its closest neighbors, without competition at all with the other species. Then if $a < 1$ is the measure of niche overlap for two adjacent niches, then the competition matrix has the form

$$A = \begin{Vmatrix} 1 & a & & & 0 \\ a & 1 & a & & \\ & \cdot & \cdot & \cdot & \\ & & \cdot & \cdot & \cdot \\ & & a & 1 & a \\ 0 & & & a & 1 \end{Vmatrix}. \tag{6.21}$$

Clearly, in that case a cannot be arbitrarily close to 1, since if the 1st species has more overlap with the 2nd, whereas the 2nd overlaps to the same extent with the 3rd, then inevitably the 1st and the 3rd species also have an overlap.

In another particular case, when every species equally competes with all the rest, the competition matrix has the form

$$A = \begin{Vmatrix} 1 & a & a & \dots & a \\ a & 1 & a & \dots & a \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ a & a & a & \dots & 1 \end{Vmatrix}. \tag{6.22}$$

This case is realized, for instance, for three species with identical niches centered at vertices of an equilateral triangle on a two-dimensional resource spectrum; or for 4 species with their niche centers at vertices of a regular tetrahedron in a three-dimensional resource space; or, in the general case, by n species with niche centers at vertices of a regular n-hedron, a simplex spanned on $n - 1$ equal vectors, in an $(n - 1)$-dimensional space of resource.

Since both these matrices may be constructed in terms of specially chosen resource spectrum and utilization functions, *apriori* one may assert that they are positive definite, that is, the corresponding competitive communities are dissipative. Nevertheless, it is of particular interest to compute the eigenvalues to know how fast the perturbed trajectories converge to an equilibrium.

Matrix (6.21) has already been studied by Laplace. Its nth degree characteristic polynomial $D_n(\lambda)$ enjoys the recurrence property

$$D_n(\lambda) = (1 - \lambda) D_{n-1}(\lambda) - a^2 D_{n-2}(\lambda).$$

The solution to this difference equation may be written in the form

$$D_n(\lambda) = a^n \frac{\sin(n+1)\theta}{\sin\theta}, \qquad \cos\theta = \frac{1-\lambda}{2a}. \tag{6.23}$$

Tackling the equation $D_n(\lambda) = 0$ we get

$$\lambda_k = 1 - 2a\cos\frac{\pi k}{n+1}, \qquad k = 1, 2, \ldots, n, \tag{6.24}$$

whence, in particular, it follows that for a competitive pattern (6.21) to exist (when it results from the integral representation (6.6)), the overlap of adjacent niches should measure less than

$$a_{\max} = 1\Big/\left(2\cos\frac{\pi}{n+1}\right),$$

the latter tending to 1/2 for large n.

Matrix (6.22) is a special case of a matrix, every row of which, starting from the second one, is derived from the preceding row by a cyclic shift of entries by one number. A matrix of this kind is termed *cyclic* or *circulant* matrix. If its first row elements are denoted $c_0, c_1, \ldots, c_{n-1}$, then the eigenvalues are*

$$\lambda_k = c_0 + c_1\varepsilon_k + c_2\varepsilon_k^2 + \ldots + c_{n-1}\varepsilon_k^{n-1}, \qquad k = 0, 1, \ldots, n-1, \tag{6.25}$$

where ε_k is the kth root of the equation $\varepsilon^n = 1$. If a cyclic matrix is yet symmetric, then λ_k are real, and hence when ε_k are in a trigonometrical form, only cosine terms are to remain in the sum of (6.25), that is,

$$\lambda_k = c_0 + c_1\cos\varphi_k + c_2\cos 2\varphi_k + \ldots + c_{n-1}\cos(n-1)\varphi_k,$$
$$k = 0, 1, \ldots, n-1; \qquad \varphi_k = 2\pi k/n. \tag{6.26}$$

It follows that the spectrum of matrix (6.22) consists of numbers

$\lambda = 1 - a$ with multiplicity $(n-1)$,

$\lambda = 1 + (n-1)a$ once.

Consider now the case where niche overlap steadily decreases with species separation in the resource space. An analytical examination may be performed in the case

$$\alpha_{ij} = a^{|i-j|}, \qquad 0 < a < 1, \tag{6.27}$$

* Cf., for instance, R. Bellman, *Introduction to Matrix Analysis*, McGraw-Hill, New York, 1960.

where a still characterizes the overlap of two adjacent niches. Then

$$A = \begin{Vmatrix} 1 & a & a^2 & \dots & a^{n-1} \\ a & 1 & a & \dots & a^{n-2} \\ a^2 & a & 1 & \dots & a^{n-3} \\ \dots & \dots & \dots & \dots & \dots \\ a^{n-1} & a^{n-2} & a^{n-3} & \dots & 1 \end{Vmatrix} \tag{6.28}$$

and expanding the $n \times n$ determinant A in elements of the first row, one may get the recurrence relation

$$\det A = D_n = (1 - a^2) D_{n-1},$$

hence

$$D_n = (1 - a^2)^{n-1} > 0 \tag{6.29}$$

for all a, $0 \leqslant a < 1$. Inequality (6.29) for $n = 1, 2, \dots$ implies that the Silvester criterion for A to be positive definite is met, and hence the competitive community with matrix (6.28) is again dissipative.

The solution to the steady-state system has the form

$$\begin{aligned} N_1^* &= \frac{K_1 - aK_2}{1-a^2}, \qquad N_n^* = \frac{K_n - aK_{n-1}}{1-a^2}, \\ N_i^* &= \frac{K_i(1+a^2) - a(K_{i-1} + K_{i+1})}{1-a^2}, \qquad i = 2, 3, \dots, n-1, \end{aligned} \tag{6.30}$$

this can be easily shown, say, by induction in n. It is peculiar for this distribution that though every species competes with all the rest, its population at the steady point is related only to the capacities of its own niche and of the two adjacent ones. From (6.24) follow the conditions for niche capacities K_i, which ensure that $\mathbf{N}^*$ is positive:

$$\begin{aligned} &K_1 - aK_2 > 0, \\ &K_i(1 + a^2) - a(K_{i-1} + K_{i+1}) > 0, \quad i = 2, 3, \dots, n-2, \\ &K_n - aK_{n-1} > 0. \end{aligned} \tag{6.31}$$

Summing up in succession the inequalities of this system (the first one with the second one divided through by a; the result multiplied by a with the third inequality divided through by a, and so on) we obtain the conditions

$$K_{i+1} < K_i/a, \qquad i = 1, 2, \dots, n-1.$$

A similar process, initiated from the last inequalities of (6.31) yields

$$aK_{n-i} < K_{n-i+1}, \qquad i = 1, 2, \dots, n-1,$$

hence, with regard to the foregoing, it follows that

$$aK_i < K_{i+1} < K_i/a, \qquad i = 1, 2, \dots, n-1. \tag{6.32}$$

Clearly, if the equilibrium is required to stay positive for any value $a \to 1$, i.e. for species packed arbitrary close, then necessarily

$$K_1 = K_2 = \ldots = K_n = K > 0. \tag{6.33}$$

In that case from (6.30) it follows that when $a \to 1$, the populations of the "boundary" species N_1^*, N_n^* approach $K/2$, whereas the populations of "intermediate" species N_i^* approach zero. The total population of n species

$$K\frac{n(1-a)+2a}{1+a}$$

steadily declines and approaches K as $a \to 1$.

Another special case of decreasing competition coefficients (6.17), that is,

$$\alpha_{ij} = [1 + |i - j|^p]^{-1},$$

$$p > 0 \tag{6.34}$$

is not amenable to analitical treatment; however, computer runs for different p and n values indicate that both the steady-state system solution [with the right-hand sides of (6.33)], and the spectrum of matrix A are positive, therefore the competitive community with matrix (6.34) is dissipative and has an equilibrium if, say, all the niche capacities are equal.

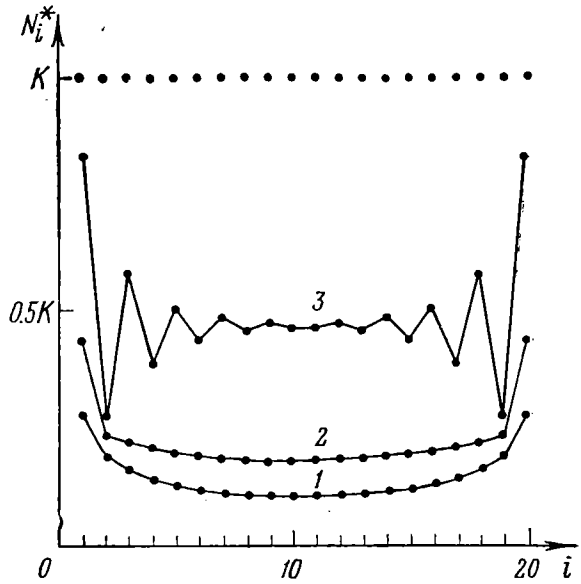

Fig. 42. Steady-state distribution of populations in $n = 20$ species for competition coefficients from (6.34) with different values of parameter p: 1—$p = 1/2$; 2—$p = 1$; 3—$p = 4$.

Analysing the results of computer-aided studies, we can make some qualitative conclusions as to populations distributions at the stationary point. In part these results are presented in Fig. 42. It turns out that the higher the values of p, i.e. the faster the decline in competition as we pass from one niche to the next one, the higher the mean equilibrium populations. For parameter values $p = 2$ or more the solution exhibits damped stable oscillations, and the less the p values, the faster they are damped (with increasing number). For $p \leqslant 1$ the solution is U-shaped: there is a steady decrease from boundaries to the centre.

6.4. Positive and partially positive equilibrium states

In the examples considered above the competition matrices appeared to be dissipative, so that the stability problem for the community amounted to finding whether or not the system (6.7) with a given

set of niche capacities has an equilibrium $\mathbf{N}^*$, such that all its coordinates $N_i^* > 0$. And what can be said about equilibrium with a part of their coordinates being zero? (Such points will be termed *partially positive*.)

Stability analysis of these points is of importance in the context of the following ecological problem. Suppose a steadily existing community is invaded by a small amount of organisms of some new species. When will the new species establish themselves in the community, and when should we expect them to decline to extinction? Clearly, the first outcome is possible only if the appropriate partially positive stationary point is unstable in the expanded community, with the positive equilibrium being stable. If the partially positive point is stable (against perturbations of any of its coordinates), then the new species will become extinct in the community.

For dissipative communities the answer is straightforward. As long as any species subsystem in a dissipative community again makes up a dissipative system, any partially positive point is stable whereas its positive coordinates are perturbed, and loses stability when zero coordinates are affected by perturbation, and in case the new species set features an equilibrium, the displaced trajectory approaches exactly this equilibrium, while otherwise it tends to other partially positive points.

Thus, any set of species may exist in a dissipative community (if only the niche capacities provide for the appropriate partially positive equilibrium), and invaders of new species secure themselves in the community (with the same condition).

In a more general case a special study is needed; the following "geometric" interpretation of equilibria positiveness helps in carrying it out.

Let $A = \| a_{ij} \|$ be a non-negative ($a_{ij} \geqslant 0$) non-singular $n \times n$ matrix, P^n—the positive orthant of the n-dimensional space, $\mathbf{e}_1, \ldots, \mathbf{e}_n$—the vectors of an orthonormalized basis. Consider the image of P^n when linearly transformed by matrix A. The orthant P^n consists of vectors of the form

$$\mathbf{x} = x_1\mathbf{e}_1 + \ldots + x_n\mathbf{e}_n,$$

where $x_i \geqslant 0$. The transformation A transfers basis vectors into columns of matrix A: $A\mathbf{e}_j = [a_{1j}, a_{2j}, \ldots, a_{nj}]^T$ (which are linearly independent due to A non-singularity), and any vector $\mathbf{x} \in P^n$ is transferred into their linear combination with non-negative coefficients:

$$A\mathbf{x} = \sum_{j=1}^{n} x_j A\mathbf{e}_j.$$

Thus the orthant P^n is shrinked by the transformation A into an n-hedral angle AP^n with the generatrices $A\mathbf{e}_j$. The existence of

a positive solution to system

$$Ax = \mathbf{K}, \qquad \mathbf{K} > 0 \tag{6.35}$$

implies that vector $\mathbf{K}$ belongs to the angular region AP^n, since a continuous transformation A^{-1} transfers an interior point of AP^n into an interior point of P^n (all components x_i are positive).

Since A is linear, vectors $\mathbf{K}$, which give a positive solution to (6.35), may be determined up to a positive constant factor, i.e. they are only determined by their direction, so that all the variety

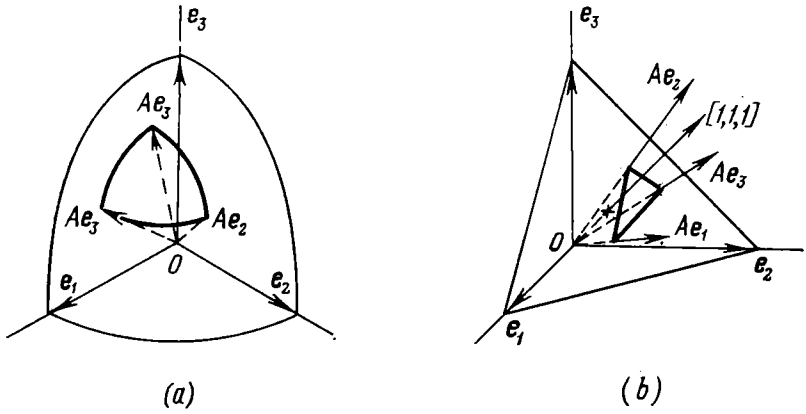

Fig. 43. An illustration to the definition of the "equilibrium" measure for the competition matrix A ($n = 3$); (a) in Euclidean matrices; (b) for the norm $\| \mathbf{x} \|\Sigma = | x_1 | + | x_2 | + | x_3 |$ (the direction $\mathbf{K} = [1, 1, 1]$ lies beyond the simplex $\sigma^3 (A)$.

of vectors of this kind may be restricted by the requirement that, say, the Euclidean norm $\| K \|$ be equal to 1. Then these vectors ends lie on a sphere S^n of a unit radius, and the n-hedral angle AP^n cuts out a spherical n-hedron s^n (A) on its surface, comprised by "arcs" of (n — 1)-dimensional circles, their hyperplanes passing through the origin (Fig. 43a). The volume s^n (A) (which is actually the area in the 3-D case) specifies the number of directions in P^n, which belong to positive equilibriums; and, if related to the $(1/2^n)$th fraction of the volume confined within S^n, it can give a measure of equilibrium for competition matrix A. For dissipative systems, because their stability is reduced to the existence of a positive equilibrium, the quantity μ (A) is simply a stability measure for a competitive pattern. Clearly μ (A) = 1 only when $A = D$, where D is a diagonal positive matrix of a scaling transformation, associated with a community of n non-interacting species with self-limitation, which is stable for any values $K_i > 0$. The smaller the value of μ (A), the fewer the number of sets for K_i, which provide that the equilibrium is positive.

For $n = 3$ this measure is calculated as follows

$$\mu(A) = s^3(A) \Big/ \left(\frac{1}{8} 4\pi\right) = 2s^3(A)/\pi, \tag{6.36}$$

where the area of the spherical triangle is

$$s^3(A) = A + B + C - \pi,$$

A, B, and C are the angles of the spherical triangle in radians*.

If a, b, and c are the sides (arches) of the triangle, which are opposite to these angles, then by formulas of analytical geometry we easily obtain

$$\cos a = \frac{a_{11}a_{12} + a_{21}a_{22} + a_{31}a_{32}}{\sqrt{a_{11}^2 + a_{21}^2 + a_{31}^2}\sqrt{a_{12}^2 + a_{22}^2 + a_{32}^2}},$$

$$\cos b = \ldots, \qquad \cos c = \ldots,$$

then by formulas of a spherical triangle** we may find the angles A, B and C, and then calculate the area s^3. The reader is encouraged to generalize the given scheme to the case of an arbitrary n.

If instead of the Euclidean vector norm we use the norm

$$\| \mathbf{x} \|_\Sigma = | x_1 | + | x_2 | + \ldots + | x_n |,$$

then the restriction $\| \mathbf{K} \|_\Sigma = 1$, in place of the sphere, gives an $(n - 1)$-dimensional simplex Σ^n built on basis vectors (Fig. 43*b*), an aggregate of all possible convex linear combinations, or a *convex hull*, of vectors $\mathbf{e}_1, \ldots, \mathbf{e}_n$:

$$\mathbf{x} = \lambda_1\mathbf{e}_1 + \lambda_2\mathbf{e}_2 + \ldots + \lambda_n\mathbf{e}_n, \quad \lambda_j \geqslant 0, \quad \lambda_1 + \ldots + \lambda_n = 1.$$

Then the n-hedral angle AP^n cuts out another simplex on this simplex, $\sigma^n \subset \Sigma^n$, which is spanned on normalized vectors $A\mathbf{e}_1, \ldots, A\mathbf{e}_n$ and the ratio of "areas" serves as a measure of equilibrium (or stability in the dissipative case) in the competitive pattern:

$$\mu_\Sigma(A) = \sigma^n(A)/\Sigma^n. \tag{6.37}$$

For $n = 3$ the simplex area equals up to a sign to

$$\sigma^3(A) = \frac{1}{2\rho} \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} (\| A\mathbf{e}_1 \|_\Sigma \cdot \| A\mathbf{e}_2 \|_\Sigma \cdot \| A\mathbf{e}_3 \|_\Sigma)^{-1},$$

where ρ is the distance from the simplex plane to the origin, $\rho = 1/\sqrt{3}$ and $\| A\mathbf{e}_j \|_\Sigma$ by definition is the sum of absolute values of

* Cf. Korn G. A., Korn T. M., *Mathematical handbook for scientists and engineers*, McGraw-Hill, New York, 1968, Section 1.12-2.

** Cf. Korn G. A., Korn T. M., *Mathematical handbook for scientists and engineers*, McGraw-Hill, New York, 1968, Section 1.12-2.

elements in the jth column of A. Hence,

$$\mu_\Sigma(A) = \frac{\sigma^3(A)}{\Sigma^3} = \frac{|\det A|}{\|Ae_1\|_\Sigma \cdot \|Ae_2\|_\Sigma \cdot \|Ae_3\|_\Sigma}. \tag{6.38}$$

For the competition matrix A with pattern (6.17) this gives

$$\mu_\Sigma\left(\left\|\begin{matrix} 1 & \alpha & \beta \\ \alpha & 1 & \alpha \\ \beta & \alpha & 1 \end{matrix}\right\|\right) = \frac{(1-\beta)(1+\beta-2\alpha^2)}{(1+\alpha+\beta)^2(1+2\alpha)}. \tag{6.39}$$

In view of these interpretations it becomes apparent that statements of the kind: "If there exists a positive equilibrium, then it is to be stable", may not be true in a more general case than the dissipative one. In fact, one can easily think of a community matrix which is not stable. Yet any matrix A with non-negative entries produces a non-empty angle $AP^n \subset P^n$, i.e. there exist vectors $\mathbf{K}$, such that they give a positive stationary point, which is unstable by the choice of matrix A.

It is also clear how system (6.7) with a fixed set of K_i may lose equilibrium, when the species packing is made more close; this fact has been mentioned in Section 6.2 for a concrete pattern (6.14). For values of a sufficiently close to 1, the simplex $\sigma^n(A)$ (as well as the spherical n-hedron s^n) shrinks to such an extent, that vector $\mathbf{K} = [1, 1, \ldots, 1]$ falls beyond its boundary (Fig. 43*b*); the stability measures μ and μ_Σ [cf. (6.39)] approaching zero in this case.

Return now to *partially positive* equilibrium points. Being solutions to the system

$$N_i\left(\sum_{j=1}^{n} \alpha_{ij}N_j - K_i\right) = 0, \qquad i = 1, \ldots, n, \tag{6.40}$$

they may have zeros in any of their coordinate places, and the non-zero coordinates are solutions to the linear system with matrix A', which is derived from matrix A by canceling the rows and columns with the numbers of zero coordinates ("truncated" matrix). Clearly, the largest number of all possible points is 2^n (this includes the point $\mathbf{0}$ and the positive equilibrium $\mathbf{N}^*$). The question arises of whether there always exists a positive solution to the "truncated" system

$$A'\mathbf{N}' = \mathbf{K}'. \tag{6.41}$$

The cancellation of any m rows and the corresponding columns from the original matrix ($m = 1, \ldots, n-1$) indicates that the linear operator A is narrowed to the subspace R^{n-m}, and the transition to the truncated system (6.41) implies projection of the right-hand side vector $\mathbf{K}$ onto R^{n-m}. If the projection operator is denoted by p_m, then for the projection of the n-hedral angle we write $p_m AP^n$

and $A'P^{n-m}$ is the $(n-m)$-hedral angle we get when the orthant P^{n-m} shrinks by the transformation A' (when A' is a non-singular matrix). It is easy to prove that in the general case

$$p_m A P^n \supset A' P^{n-m} \tag{6.42}$$

and $p_m A P^n \setminus A' P^{n-m}$, generally speaking, is non-empty. In fact, if $\mathbf{x}' = [x_{j_1}, \ldots, x_{j_{n-m}}] \in P^{n-m}$, then

$$A'\mathbf{x}' = \sum_{k=1}^{n-m} x_{j_k} A \mathbf{e}'_{j_k},$$

and if vector $\mathbf{x}'$ is supplemented to vector $\mathbf{x} \in P^n$ by zero coordinates, then

$$A'\mathbf{x}' = p_m A \mathbf{x}.$$

Clearly, the necessary and sufficient condition for the positive solution to the truncated system (6.41) to exist is the condition that the projection of vector $\mathbf{K}$ should fall within the $(n-m)$-hedral angle:

$$\mathbf{K}' = p_m \mathbf{K} \in A' P^{n-m}. \tag{6.43}$$

For matrices of horizontally structured communities there may be cases when $p_m A P^n$ is actually wider than $A' P^{n-m}$ (cf. Example 1 later in this section), i.e. there exist vectors $\mathbf{K} \in A P^n$ (yielding a positive equilibrium), for which condition (6.43) is not satisfied and the truncated system has no positive solutions.

On the other hand, vectors $\mathbf{K}$ are possible, such that the solutions to (6.41) are positive no matter how the original matrix A was truncated, i.e. condition (6.43) holds for any operator p_m. In Example 2 considered below, this is traced for matrix A of (6.17) and vector $\mathbf{K} = [1, \ldots, 1]$ when $n = 4$, i.e. in this case the community has all the $2^4 = 16$ steady-state points.

The requirement that there exist a positive solution to the truncated system for any vector $\mathbf{K} > 0$, which leads to a positive solution to the original system (6.35), implies in terms of our geometric interpretation that the projection of the n-hedral angle AP^n coincides with the $(n-m)$-hedral angle $A'P^{n-m}$:

$$p_m A P^n = A' P^{n-m}. \tag{6.44}$$

If the transformation A is non-singular, then the generatrices of the angle $A'P^{n-m}$ (matrix A' columns) forms a basis in P^{n-m}. Condition (6.44) indicates then that the projections of generatrices of angle AP^n, which belong to the "truncated" coordinates, i.e. $p_m A \mathbf{e}_{i_1}, \ldots, p_m A \mathbf{e}_{i_m}$, may be linearly expressed (with non-negative coefficients) in terms of the generatrices of the angle $A'P^{n-m}$. This in turn is equivalent to each of the systems

$$A'\mathbf{x} = p_m A \mathbf{e}_{i_k}, \qquad k = i, \ldots, m, \tag{6.45}$$

having a non-negative solution. The latter, by Cramer's rule for a linear system solution, requires that the signs of all non-zero determinants, we get from matrix A' by substituting some vector $p_m A e_{i_k}$ for one of its columns, coincide with the sign of det A'. This takes place when $n = 4$ and $m = 1, 2, 3$ for matrix A of the (6.28) form (Example 3), i.e. if only this model has a positive equilibrium $\mathbf{N}^*$, then there exist all the 15 partially positive steady-state points.

Example 1. To see that condition (6.44) may well be failed, consider a 4×4 competition matrix (6.17):

$$A = \begin{Vmatrix} 1 & \alpha & \beta & \gamma \\ \alpha & 1 & \alpha & \beta \\ \beta & \alpha & 1 & \alpha \\ \gamma & \beta & \alpha & 1 \end{Vmatrix}, \qquad \det A \neq 0. \tag{6.46}$$

Suppose the last coordinate is zeroed, that is, the last row and column are cancelled. For vector $p_1 A e_4 = [\gamma, \beta, \alpha]^T$ to be a linear non-negative combination of generatrices of the angle $A'P^3$, which are columns of matrix A', it is necessary and sufficient for the system of equations

$$\begin{Vmatrix} 1 & \alpha & \beta \\ \alpha & 1 & \alpha \\ \beta & \alpha & 1 \end{Vmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} = \begin{bmatrix} \gamma \\ \beta \\ \alpha \end{bmatrix} \tag{6.47}$$

to have a non-negative solution. The system determinant is

$$D' = (1 - \beta)(1 + \beta + 2\alpha^2),$$

and the determinant which belongs to x_1

$$D^{(1)} = \alpha^3 + \alpha\beta + \gamma - \alpha^2\gamma - 2\alpha\beta < 0,$$

say, for $\alpha = 0.7$, $\beta = 0.5$, $\gamma = 0.31$, when D is positive. Thus, $x_1 < 0$ and condition (6.44) is not satisfied, and therefore it might be that even though there is a positive equilibrium, the partially positive steady point belonging to matrix A' of (6.47) will be lacking. This case is realized, for instance, for the vector $\mathbf{K} = [\gamma, \beta, \alpha, K_4]$, $0 < K_4 < 1$.

Example 2. Consider now all sorts of truncations for system

$$\begin{Vmatrix} 1 & \alpha & \beta & \gamma \\ \alpha & 1 & \alpha & \beta \\ \beta & \alpha & 1 & \alpha \\ \gamma & \beta & \alpha & 1 \end{Vmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \end{bmatrix} \tag{6.48}$$

supposing that

$$1 > \alpha > \beta > \gamma > 0. \tag{6.49}$$

If the first or fourth coordinate is zeroed, the truncated matrix has the form

$$A' = \begin{Vmatrix} 1 & \alpha & \beta \\ \alpha & 1 & \alpha \\ \beta & \alpha & 1 \end{Vmatrix},$$

and the condition which ensures positiveness of the solution to $A'\mathbf{x}' = [1, 1, 1]^T$ is

$$\alpha < (1 + \beta)/2. \tag{6.50}$$

When the second coordinate is zeroed, the truncated system appears in the form

$$\begin{Vmatrix} 1 & \beta & \gamma \\ \beta & 1 & \alpha \\ \gamma & \alpha & 1 \end{Vmatrix} \begin{bmatrix} x_1 \\ x_3 \\ x_4 \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix}.$$

For the determinant of this system

$$D' = 1 + 2\alpha\beta\gamma - \alpha^2 - \beta^2 - \gamma^2$$

to be positive, for instance, the condition

$$\alpha^2 < (1 + \gamma)/2 \tag{6.51}$$

is sufficient. Determinants, which belong to x_1, x_3, x_4 are

$$D^{(1)} = 1 + \alpha\beta + \alpha\gamma - \gamma - \alpha^2 - \beta,$$
$$D^{(3)} = 1 + \alpha\gamma + \beta\gamma - \gamma^2 - \alpha - \beta,$$
$$D^{(4)} = 1 + \alpha\beta + \beta\gamma - \gamma - \alpha - \beta^2.$$

Since

$$\frac{\partial D^{(1)}}{\partial \alpha} = \beta + \gamma - 2\alpha, \qquad \frac{\partial D^{(1)}}{\partial \beta} = \alpha - 1, \qquad \frac{\partial D^{(1)}}{\partial \gamma} = \alpha - 1,$$

the set of extremal points for determinant $D^{(1)}$ in the space of parameters (α, β, γ) obviously has no intersection with the bounded domain Ω, defined by conditions (6.49). Yet $D^{(1)} \geqslant 0$ on the boundaries of Ω and we can find points within Ω where $D^{(1)} > 0$. Hence, as long as $D^{(1)}$ may be continuously differentiated with respect to α, β, γ we can deduce that $D^{(1)} > 0$ everywhere within Ω. With an additional restriction

$$\beta < (\alpha + \gamma)/2 \tag{6.52}$$

it may be proved in a like manner that $D^{(3)}$ and $D^{(4)}$ are positive. Thus, within the intersection of Ω and the domains assigned by (6.50)-(6.52), denote it by $\tilde{\Omega}$, the solutions of the given truncated system are positive.

The restrictions on the domain $\tilde{\Omega}$ are already sufficient to get positive solutions when the original system is truncated in the 3rd coordinate. When the truncation is made in any two or three coordinates, the solution is obviously positive in $\tilde{\Omega}$.

Thus, competition matrix (6.46) with the set of niche capacities $\mathbf{K} = [1, 1, 1, 1]$ (or proportional to $\mathbf{K}$) yields a partially positive solution in the parameters domains $\tilde{\Omega}$ for any kind of truncation. That $\tilde{\Omega}$ is non-empty is readily seen from the example of numerical values for α, β, γ which appeared when studying subsystem (6.47).

Example 3. In the special case of (6.27) matrix (6.46) is reduced to the positive definite matrix

$$A = \begin{Vmatrix} 1 & a & a^2 & a^3 \\ a & 1 & a & a^2 \\ a^2 & a & 1 & a \\ a^3 & a^2 & a & 1 \end{Vmatrix}, \qquad 0 < a < 1. \tag{6.53}$$

Zeroing the 1st coordinate we get

$$A' = \begin{Vmatrix} 1 & a & a^2 \\ a & 1 & a \\ a^2 & a & 1 \end{Vmatrix}$$

and $D' = \det A' > 0$. The determinants for the unknowns are

$$D^{(2)} = aD' > 0, \qquad D^{(3)} = 0, \qquad D^{(4)} = 0.$$

Likewise, for all other truncations of (6.53) $D^{(j)} \geqslant 0$. This means, that for matrix (6.53) the inclusion of (6.42) is actually reduced to the inequality (6.44), i.e. if there exists a positive equilibrium point, then there exist all the rest of $2^4 - 1 = 15$ partially positive equilibria.

6.5. Linear programming in examination of competition matrix

As mentioned in Section 6.3, the specific structure of (6.17) for a competition matrix is still insufficient for the latter to be positive definite, and hence for the competitive community to be dissipative. We cannot write out the eigenvalues of matrix A in a general form or to prove their positiveness in the general case using localization criteria such as Gershgorin circles or ovals of Cassini, etc.

We introduce the following restriction on the manner in which competition coefficients decrease when species are farther and farther separated in the resource space. Suppose the declining function of integral argument $\alpha(z) > 0$ meets the conditions of strict convexity:

$$\alpha(m) < \frac{1}{2}[\alpha(m-1) + \alpha(m+1)],$$

$$m = 1, \ldots, n-1. \tag{6.54}$$

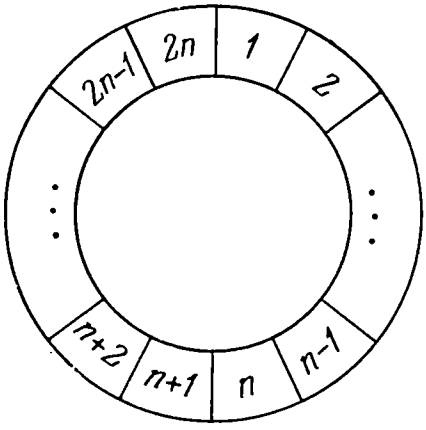

Fig. 44. Diagram of the annular arrangement of ecological niches.

In what follows we shall prove

Theorem 2. Matrix $A = \| \alpha_{ij} \|$ *with entries* $\alpha_{ij} = \alpha(|i-j|)$, *that satisfy conditions* (6.54), *is positive definite.*

To begin with consider the special case of niche arrangement, illustrated in Fig. 44, though somewhat artificial, it will serve the purposes of our future analysis. Clearly, in this case the competition coefficients of one species with the others first decline to a certain extent and then grow in a reverse manner.

Denoting $\alpha(m) = \alpha_m$ and supposing that $\alpha(0) = 1$, we can write down the competition matrix for a ring community in the form

$$C(A) = \left\| \begin{array}{cccccc|ccc} 1 & \alpha_1 & \alpha_2 & \ldots & \alpha_{n-1} & \alpha_n & \alpha_{n-1} & \ldots & \alpha_1 \\ \alpha_1 & 1 & \alpha_1 & \ldots & \alpha_{n-2} & \alpha_{n-1} & \alpha_n & \ldots & \alpha_2 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \alpha_{n-1} & \alpha_{n-2} & \alpha_{n-3} & \ldots & 1 & \alpha_1 & \alpha_2 & \ldots & \alpha_n \\ \alpha_n & \alpha_{n-1} & \alpha_{n-2} & \ldots & \alpha_1 & 1 & \alpha_1 & \ldots & \alpha_{n-1} \\ \hline \alpha_{n-1} & \alpha_{n-2} & \alpha_{n-3} & \ldots & \alpha_2 & \alpha_1 & 1 & \ldots & \alpha_{n-2} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \alpha_1 & \alpha_2 & \alpha_3 & \ldots & \alpha_n & \alpha_{n-1} & \alpha_{n-2} & \ldots & 1 \end{array} \right\| \left.\vphantom{\begin{array}{c}1\\1\\1\\1\\1\end{array}}\right\} (n+1) \text{ rows}. \tag{6.55}$$

Matrix $C(A)$ is cyclic and symmetric, and its submatrix A, made up by the first $n+1$ rows and columns belongs to an ordinary horizontally structured community. Clearly, matrix A is symmetric if and only if the circulant $C(A)$ is symmetric. Notice by the way that any symmetric $2n \times 2n$ circulant is uniquely determined by the set of the first $n+1$ entries in the first row, and has the pattern of (6.55).

Since the sum of entries in each row of $C(A)$ is the same, the positive steady point $\mathbf{N}^*$ for equal right-hand sides in equations of

$C(A)\mathbf{N}^* = \mathbf{K}$ ($\mathbf{K} = [K, \ldots, K]$, will have equal components

$$N_i^* = \frac{K}{1+2(\alpha_1+\alpha_2+\ldots+\alpha_{n-1})+\alpha_n}, \qquad i=1, 2, \ldots, 2n. \tag{6.56}$$

According to (6.26) the eigenvalues of $C(A)$ are

$$\begin{gathered}\mu_k = 1 + 2\sum_{j=1}^{n-1} \alpha_j \cos j\varphi_k + (-1)^k \alpha_n, \\ k=0, 1, \ldots, 2n-1; \qquad \varphi_k = \pi k/n,\end{gathered} \tag{6.57}$$

and it can be easily shown that

$$\mu_k = \mu_{2n-k}, \qquad k = 1, 2, \ldots, n-1.$$

Thus, in order to prove that $C(A)$ is positive definite we need to check the conditions

$$\mu_k = 1 + 2\sum_{j=1}^{n} \alpha_j \cos j\varphi_k + (-1)^k \alpha_n > 0, \qquad k=0, 1, \ldots, n, \tag{6.58}$$

under the restrictions

$$1 > \alpha_1 > \alpha_2 > \ldots > \alpha_n > 0, \tag{6.59}$$

$$\alpha_m < \frac{1}{2}(\alpha_{m-1} + \alpha_{m+1}), \qquad m=1, \ldots, n-1. \tag{6.60}$$

Notice that there is a linear function of variables α_j in the left-hand side of inequality (6.58), and the restrictions (6.59) and (6.60) are of the same kind as in problems of linear programming, with the only difference that the latter comprise inequalities which are not strict. Denote

$$\Omega = \Big\{(\alpha_1, \ldots, \alpha_n): 1 > \alpha_1 > \ldots > \alpha_n > 0; \\ \alpha_m < \frac{1}{2}(\alpha_{m-1} + \alpha_{m+1}),\ m=1, 2, \ldots, n-1\Big\},$$

$$\bar{\Omega} = \Big\{(\alpha_1, \ldots, \alpha_n): 1 \geqslant \alpha_1 \geqslant \ldots \geqslant \alpha_n \geqslant 0; \\ \alpha_m \leqslant \frac{1}{2}(\alpha_{m-1} + \alpha_{m+1}),\ m=1, 2, \ldots, n-1\Big\}.$$

Clearly then $\bar{\Omega} \supset \Omega$ and

$$\inf_{\Omega} \mu_k \geqslant \min_{\bar{\Omega}} \mu_k, \qquad k=0, 1, \ldots, n. \tag{6.61}$$

The minimization problem for μ_k on the set $\bar{\Omega}$ represents a classic problem of linear programming, and further on by methods of this

theory it will be shown that, first,

$$\min_{\bar{\Omega},\, k} \mu_k = 0,$$

second, that this minimum is not attained at any point of the open set Ω, and third, that

$$\inf_{\Omega} \{\min_{k} \mu_k\} = 0.$$

To reduce the minimization of μ_k to the problem of linear programming in its standard form, introduce the new variables x_j, connected with the original α_j by formulas

$$\begin{aligned}
1 = \alpha_0 &= x_0 + 2x_1 + \ldots + nx_{n-1} + x_n, \\
\alpha_1 &= x_1 + 2x_2 + \ldots + (n-1)x_{n-1} + x_n, \\
&\ldots \\
\alpha_m &= x_m + 2x_{m+1} + \ldots + (n-m)\, x_{n-1} + x_n, \\
&\ldots \\
\alpha_{n-1} &= x_{n-1} + x_n, \\
\alpha_n &= x_n.
\end{aligned} \tag{6.62}$$

Then from conditions (6.60) it follows that

$$x_{m-1} \geqslant 0, \qquad m = 1,\ 2,\ \ldots,\ n-1,$$

and the condition $\alpha_{n-1} \geqslant \alpha_n \geqslant 0$ leads to $x_{n-1} \geqslant 0$, $x_n \geqslant 0$. Eventually, we get the linear programming problem in the standard form: find the minimum to the linear form μ_k (x) with one restricting equality

$$x_0 + 2x_1 + \ldots + nx_{n-1} + x_n = 1 \tag{6.63}$$

and $n + 1$ restricting inequalities

$$x_m \geqslant 0, \qquad m = 0,\ 1,\ \ldots,\ n. \tag{6.64}$$

It has been known*, that the solution to a linear programming problem is attained in one or several vertices of simplex $\bar{\Omega}$, defined by conditions (6.63)-(6.64). In the last case every point of a convex set spanned on vertices that minimize the linear form is also a solution in the latter case.

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* See, for instance, Korn G. A., Korn T. M., *Mathematical handbook*, McGraw-Hill, New York, 1968, Section 11.4-1.

In the space of variables x_j the vertices of simplex $\overline{\Omega}$ have the following coordinates:

$$\mathbf{V}_0 = [1, 0, 0, \ldots, 0, 0],$$
$$\mathbf{V}_1 = [0, 1/2, 0, \ldots, 0, 0],$$
$$\cdots\cdots\cdots\cdots\cdots\cdots$$
$$\mathbf{V}_{n-1} = [0, 0, 0, \ldots, 1/n, 0],$$
$$\mathbf{V}_n = [0, 0, 0, \ldots, 0, 1],$$

whereas in the space of variables $[\alpha_1, \ldots, \alpha_n]$, with regard to formulas (6.62) the coordinates are

$$\mathbf{V}_0 = [0, 0, \ldots, 0],$$
$$\mathbf{V}_1 = [1/2, 0, \ldots, 0],$$
$$\cdots\cdots\cdots\cdots\cdots\cdots$$
$$\mathbf{V}_m = \left[\frac{m}{m+1}, \frac{m-1}{m+1}, \ldots, \frac{1}{m+1}, 0, \ldots, 0\right], \quad m=1, 2, \ldots, n-1,$$
$$\cdots\cdots\cdots\cdots\cdots\cdots$$
$$\mathbf{V}_n = [1, 1, \ldots, 1].$$

Evidently, the value for μ_k at the vertex $\mathbf{V}_0$ is

$$\mu_k(\mathbf{V}_0) = 1, \tag{6.65}$$

and at the vertices $\mathbf{V}_1, \ldots, \mathbf{V}_{n-1}$

$$\mu_k(\mathbf{V}_m) = 1 + 2\sum_{l=1}^{m} \frac{m+1-l}{m+1} \cos l\varphi_k = 1 + \frac{2}{m+1} Y_m(\varphi_k), \tag{6.66}$$

where we denoted

$$Y_N(\varphi) = N\cos\varphi + (N-1)\cos 2\varphi + \ldots + \cos N\varphi.$$

By method of complete mathematical induction we may show that for all admissible φ values we have

$$Y_N(\varphi) = \frac{1}{2}\left[\frac{\cos\varphi - \cos(N+1)\varphi}{1-\cos\varphi} - N\right], \qquad \varphi \neq 0, \pm 2\pi, \ldots, \tag{6.67}$$

and based on this the expression (6.66) may be rearranged to give

$$\mu_k(\mathbf{V}_m) = \frac{1}{m+1} \cdot \frac{1-\cos(m+1)\varphi_k}{1-\cos\varphi_k}, \qquad m = 1, \ldots, n-1. \tag{6.68}$$

(Notice that the denominator in (6.68) is non-zero for all φ_k, $k = 1, \ldots, n$.) From (6.68) it is apparent that for $m = 1, \ldots, n-2$

$$\mu_k(\mathbf{V}_m) > 0, \tag{6.69}$$

and for $m = n - 1$ we have

$$\mu_k(\mathbf{V}_{n-1}) = \frac{1}{n}\,\frac{1-(-1)^k}{1-\cos\varphi_k} = \begin{cases} 0, & \text{if } k \text{ is even} \\ \dfrac{2}{n(1-\cos\varphi_k)} > 0, & k \text{ is odd} \end{cases} \tag{6.70}$$

Further,*

$$\mu_k(\mathbf{V}_n) = 1 + 2\sum_{j=1}^{n-1} \cos j\varphi_k\,(-1)^k$$

$$= \frac{\sin(n-1/2)\,\varphi_k}{\sin\varphi_k/2} + (-1)^k = (-1)^{k-1} + (-1)^k = 0 \tag{6.71}$$

for all $k = 1, \ldots, n$.

Summing up (6.65) and (6.69)-(6.71) we obtain that $\min\limits_{\bar\Omega} \mu_k = 0$, $k = 1, 2, \ldots, n$ and for odd k this minimum is attained at the only point $\mathbf{V}_n$, while for even k it is attained at the vertex $\mathbf{V}_{n-1}$ as well. In the second case, by linear programming theory, $\mu_k = 0$ also at any point of the interval I between vertices $\mathbf{V}_{n-1}$ and $\mathbf{V}_n$. Thus

$$\min_k \min_{\bar\Omega} \mu_k = 0,$$

and the minimum is attained on the interval $I \subset \bar\Omega$. Any point of this interval

$$\mathbf{V} = a\mathbf{V}_{n-1} + b\mathbf{V}_n, \qquad a,\ b \geqslant 0, \qquad a + b = 1,$$

can be presented in the form

$$\mathbf{V} = \left[b + a\left(1 - \frac{1}{n}\right),\ b + a\left(1 - \frac{2}{n}\right), \ldots, b + \frac{a}{n},\ b\right],$$

with coordinates linearly decreasing with their ordinal number.

This implies that everywhere on the interval I conditions (6.60) turn into equalities, i.e. I entirely belongs to the boundary $\bar\Omega$ and $I \cap \Omega = \varnothing$. It follows that for any point of the open set Ω, that is, for any set of α_j, which satisfies the strict inequalities in (6.59)-(6.60), the eigenvalues of the circulant $C(A)$ are

$$\mu_k > 0,$$

since $\Omega \subset \bar\Omega$ and all the points of $\bar\Omega$ for which $\mu_k = 0$ belong to I.

On the other hand, from μ_k being continuous with respect to α_j, it follows that

$$\inf_{\Omega} \{\min_k \mu_k\} = 0,$$

* Here we utilize the identity

$$\cos\alpha + \cos 2\alpha + \ldots + \cos N\alpha = \frac{1}{2}\left[\frac{\sin(N+1/2)\,\alpha}{\sin\alpha/2} - 1\right], \quad \alpha \neq 0, \pm 2\pi, \ldots.$$

i.e. in the positive spectrum (6.57) of matrix $C(A)$ by the choice of coefficients α_j, one may always arrive at an arbitrarily small eigenvalue.

Now we can prove the Theorem 2 in Section 6.5. Denote by λ_i the real eigenvalues of matrix A. Notice that matrices A and $C(A)$ meet the conditions of the Strum theorem about separability of eigenvalues*, whence it follows that at least

$$\min_k \mu_k \leqslant \lambda_i \leqslant \max_k \mu_k, \qquad i = 0, 1, \ldots, n. \tag{6.72}$$

And since all the μ_k are already proved to be positive, it follows from (6.72) that the spectrum of A is positive, Q.E.D.

Thus, when competition coefficients in the structure of (6.17) have convex patterns of decline, that is, their decline is sufficiently smooth, then matrix A is positive definite and the community is dissipative. In particular, such decline patterns are inherent in the above competitive structure (6.28) and (6.34), as well as in (6.15) for values of a not too close to 1. The spectrum positiveness for these matrices illustrates Theorem 2.

Notice that the convexity of competition coefficients is connected not only with stability of the equilibrium $\mathbf{N}^*$, but also with its existence [the existence of a positive solution to system (6.35)]. Formula (6.39), for instance, indicates that when the coefficients are far enough from being convex, that is, when $\alpha \geqslant (1 + \beta)/2$ so that the expression $(1 + \beta - 2\alpha^2)$ is close to zero, the equilibrium measure μ_Σ of such a community is extremely small. In Section 6.2 some direct calculations were mentioned, performed to solve (6.35) with coefficients from (6.14) and for a values which are sufficiently close to 1, namely those, which fail to satisfy the convexity condition $a < (1 + a^4)/2$. These calculations demonstrate that positive solutions may occur in this case only for a special choice of the right-hand sides K_i, i.e. the appropriate n-hedral angle is extremely narrow (cf. Fig. 43*b*) and, in particular, does not include the direction $\mathbf{K} = [1, 1, \ldots, 1]$.

Besides, the convexity of the competition function $\alpha(m)$ turns out to be connected with the preying effect on species packing in a stable community, where competing species serve as food for predatory species (cf. Section 6.7).

6.6. Method of evaluating $\lambda_{\min}$

The relation (6.72) proved in the previous section enables us to find upper and lower estimates for the positive spectrum of A at sufficiently high values of $n \gg 1$, and thus specify how fast the perturbed

* See Bellman R., *Introduction to Matrix Analysis*, McGraw-Hill, New York, 1960.

trajectory returns to equilibrium. In fact, if the series of values of the function $\alpha(z)$ ($z = 1, 2, \ldots$) is convergent, then from (6.58) it follows that

$$1-2\alpha_1 + 2\alpha_2 - 2\alpha_3 + \ldots \leqslant \lambda(A) \leqslant 1 + 2\alpha_1 + 2\alpha_2 + 2\alpha_3 + \ldots$$

The left-hand side of this inequality is of special interest, since it gives the lower estimate of the smallest eigenvalue of A

$$\lambda_{\min} = 1 - 2\alpha_1 + 2\alpha_2 - 2\alpha_3 + \ldots,$$

which in a more compact form may be written as

$$\lambda_{\min} = \sum_{k=-\infty}^{\infty} (-1)^k \alpha_k, \qquad \alpha_{-k} = \alpha_k. \tag{6.73}$$

The method presented below makes it possible to evaluate $\lambda_{\min}$ in a number of cases, when the summation of the alternating series (6.73) is not as trivial as, say, for (6.27), which is a geometric progression. The method is based on well-known statements of the theory of functions of complex variable. If $g(z)$ is any function analytic throughout the entire z-plane, except for, perhaps, a finite number of poles, and such that $g(z)/\sin(\pi z)$ has no singularities at $z = \infty$, then by Cauchy theorem*

$$\oint_C \frac{g(z)\,dz}{\sin(\pi z)} = 2\pi i \sum_{z=z_k} \operatorname{Res}\left\{\frac{g(z)}{\sin(\pi z)}\right\}, \tag{6.74}$$

where Res $\{f(z)\}$ stands for a residue of the function at point z, the sum is taken over all the poles z_k of the integrand, and the integral is taken along either a circle with infinite radius or any other contour C enclosing all poles of the integrand. These latter split into two categories: (a) the poles of $g(z)$, denote them by $z_j = \zeta_j + i\xi_j$, and (b) the zeros of $\sin(\pi z)$, which occur at points $z = k$, where k is any integer. If $g(z)$ is analytic in a neighborhood of $z = k$ then

$$\operatorname{Res}\left\{\frac{g(k)}{\sin(\pi z)}\right\} = \frac{(-1)^k}{\pi} g(k). \tag{6.75}$$

When $z_j \neq k$ (otherwise, a special study is required), then

$$\operatorname{Res}\left\{\frac{g(z_j)}{\sin(\pi z_j)}\right\} = \frac{\operatorname{Res} g(z_j)}{\sin(\pi z_j)},$$

and, if we consider (6.75), the identity (6.74) may be rewritten as

$$\sum_k (-1)^k g(k) = \frac{1}{2i} \oint_C \frac{g(z)\,dz}{\sin(\pi z)} - \pi \sum_j \frac{\operatorname{Res} g(z_j)}{\sin(\pi z_j)}. \tag{6.76}$$

* See, for instance, Ahlors L. V., *Complex Analysis*, McGraw-Hill, New York, 1966.

If in place of $g(z)$ we insert $\alpha(z)$ which describes the decline of competition coefficients $\alpha_{ij} = \alpha(|i-j|) = \alpha_{|i-j|}$, then the relationship (6.76) in some cases enables us to evaluate $\lambda_{\min}$ in a complete form.

Example 1. In the special case of (6.14) of equal Gaussian utilization functions we have

$$\alpha(z) = \exp\{-\mu z^2\}, \tag{6.77}$$

where

$$\mu = d^2/(4w^2).$$

The function $g(z)$ is analytic throughout the z-plane, and $\alpha(z) \to 0$ on all the circle at infinity, except for the neighborhood of the imaginary axis. The second term in (6.76) vanishes and

$$\lambda_{\min} = \frac{1}{2i}\oint_C \frac{\exp\{-\mu z^2\}\,dz}{\sin \pi z} = \oint_C \frac{\exp\{-\pi z^2 - \pi i z\}\,dz}{1-\exp\{-2\pi i z\}}. \tag{6.78}$$

The contour C will be taken to enclose the real axis (Fig. 45). As $X \to \infty$ the two vertical segments of the rectangle give no contribu-

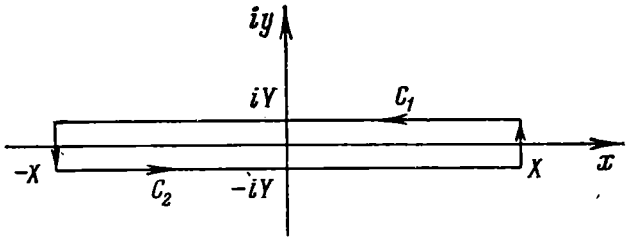

Fig. 45. Contour of integrating in the complex plane.

tion to the integral in (6.78). Next, for the line C_1 from $(+\infty, iY)$ till $(-\infty, iY)$ we have a contribution

$$J = \int_{(-\infty,\, iY)}^{(\infty,\, iY)} \frac{\exp\{-\mu z^2 + i\pi z\}\,dz}{1-\exp\{2\pi i z\}}$$

$$= \int_{-\infty}^{\infty} \frac{\exp\{-\mu x^2 - 2i\mu x\,[Y-\pi/(2\mu)] + \mu Y^2 - \pi Y\}}{1-\exp\{-2\pi Y + 2\pi i x\}}\,dx. \tag{6.79}$$

Integrating along C_2 from $(-\infty, -iY)$ to $(+\infty, -iY)$ evidently gives the complex conjugate value $\bar{J}$. Cancelling the denominator in (6.79) by expanding $(1 - \exp\{\ldots\})^{-1}$ as a sum of geometric progression, then changing variables to $s = x + i(Y - \pi/2\mu)$ in the first term, $t = x + i(Y - 3\pi/2\mu)$ — in the second, and so on, after

an appropriate rearrangement we end up with

$$\min = \int_{-\infty+iY_1}^{\infty+iY_1} \exp\left\{-\mu s^2 - \frac{\pi^2}{4\mu}\right\} ds + \int_{-\infty+iY_2}^{\infty+iY_2} \exp\left\{-\mu t^2 - \frac{9\pi^2}{4\mu}\right\} dt + \ldots + \bar{J}. \quad (6.80)$$

Finally, this gives

$$\lambda_{\min} = 2\sqrt{\frac{\pi}{\mu}} \exp\left\{-\frac{\pi^2}{4\mu}\right\} \left[1 + \exp\left\{-\frac{2\pi^2}{\mu}\right\} + \ldots\right], \quad (6.81)$$

to within notations this is the above-mentioned approximation (6.16).

Example 2. When the decline of coefficients α_{ij} is expressed by a fractional function (6.34), say, for $p = 2$, then

$$\alpha(z) = 1/(1 + z^2). \quad (6.82)$$

Function $\alpha(z)$ is analytic throughout the z-plane, except for the poles $z = \pm i$, and the integral along the circle at infinity vanishes. Residues of $\alpha(z)$ at the poles are

$$\operatorname{Res} \alpha(\pm i) = \mp i/2,$$

respectively, and so, according to (6.76)

$$\lambda_{\min} = \frac{i\pi}{\sin(i\pi)} = \frac{\pi}{\sin h\, \pi} = \frac{2\pi}{e^{\pi} - e^{-\pi}}, \quad (6.83)$$

this, in part, explains the spectrum positiveness for A with α_{ij} of the (6.34) form, which often resulted in direct calculations.

6.7. Notes and bibliography

To 6.1. A survey of different approaches to the definition of an ecological niche may be found in Chapter IX of the book:

Williamson M., *The analysis of biological populations*, Edward Arnold, London, 1972.

For comments on the Gause principle of competitive exclusion see

Maynard Smith J., *Models in ecology*, Cambridge Univ. Press, Cambridge, 1974, Chapter 5.

This principle was generalized for discrete competition models in

Shapiro A. P., "On one model of competing species", *Dokl. Acad. Nauk. USSR*, **215**, 5, pp. 1233-1235, 1974 (in Russian),

and examples of models, which fail to satisfy the principle, may be found in the works:

Armstrong R. A., MacGehee R., "Coexistence of species competing for shared resources," *Theor. Pop. Biol.*, **9**, 3, pp. 317-328, 1976;

Armstrong R. A., MacGehee R., "Coexistence of two competitors on one resource," *J. Theor. Biol.*, **56**, 2, pp. 499-502, 1976.

To 6.2. The niche formalization presented here follows the works:

MacArthur R. H., "The theory of niche." In: "*Population biology and evolution*," Ed. Lewontin R., Syracuse Univ. Press, Syracuse, pp. 159-176, 1968;

MacArthur R. H., "Species packing and competitive equilibrium for many species," *Theor. Pop. Biol.*, **1**, 1, pp. 1-11, 1970;

May R. M., MacArthur, R. H., "Niche overlap as a function of environmental variability," *Proc. Nat. Acad. Sci. USA*, **69**, 5, pp. 1109-1113, 1972.

The latter comprises analysis of the special case of equal niches (6.13), deduction of the estimate (6.16) and the proof of the limiting influence of random environmental fluctuations. This influence was also studied in:

Abrams P., "*Niche overlap and environmental variability*," *Math. Biosci.*, **28**, 3/4, pp. 357-372, 1976.

The effects of non-uniform niches and the multivariate resource spectrum are considered in:

Roughgarden J., "Evolution of niche width," *Amer. Natur.*, **106**, 952, pp. 683-718, 1972;

May R. M., "Some notes on estimating the competition matrix, α," *Ecology*, **56**, 3, pp. 737-741, 1975;

Emlen J. M., "Niches and genes: some further soughts," *Amer. Natur.*, **109**, 968, pp. 472-476, 1975;

Abrams P., "Limiting similarity and the form of the competition coefficient," *Theor. Pop. Biol.*, **8**, 3, pp. 356-375, 1975;

MacMurtrie R., "On the limit to niche overlap for nonuniform niches," *Theor. Pop. Biol.*, **10**, 1, pp. 96-107, 1976.

Analysis of Lyapunov functions, as well as their possible ecological interpretation for competitive communities, may be found in the paper:

Gilpin M. E., "A Lyapunov function for competition communities," *J. Theor. Biol.*, **44**, 1, pp. 35-48, 1974.

Competition models for cases, when competition results not only from the uptake of common resources, but also from direct conflicts between specimens (the so-called *interference*), are developed in the paper:

Case T. J., Gilpin M. E., "Interference competition and niche theory," *Proc. Nat. Acad. Sci. USA*, **71**, 8, pp. 3073-3077, 1974,

an extensive bibliography on this problem can be also found there. Stability of a more general system rather than the Volterra one, but only for two competitors, is examined in the paper:

Brauer F., "On the populations of competing species," *Math. Biosci.*, **19**, 3/4, pp. 299-306, 1974.

To 6.3. Based on the discrete analogy for the integral representation (6.6), the competition coefficients are derived, for instance in:

Levins R., *Evolution in changing environments*, Princeton Univ. Press, Princeton, 1968,

where the competition matrix (6.22) was also studied, or

Schoener T. W., "Some methods for calculating competition coefficients from resource-utilization spectra," *Amer. Natur.*, **108**, pp. 332-340, 1974.

The special case of (6.27) has been analysed in the paper:

Logofet D. O., Svirezhev Yu. M., "On Volterra models for communities of coexisting species with overlapping ecological niches," Kaliningrad, 1975, pp. 180-184. (*Theoretical and experimental biophysics*; Vol. 5.) (in Russian).

To 6.4-6.6. The proof of Theorem 2 is as in:

Logofet D. O., "On stability of one matrix class, appearing in mathematical theory of biological communities," *Dokl. Acad. Nauk. USSR*, **221**, 6, pp. 1272-1275, 1975 (in Russian).

For the relation between convexity of the competitive function α (m) and the preying effect on species packing see

Roughgarden J., Feldman M., "Species packing and predation pressure," *Ecology*, 56, 2, pp. 489-492, 1975.

The method to evaluate λ_{min} was suggested in the extensive paper on niche theory:

May R. M., "On the theory of niche overlap," *Theor. Pop. Biol.*, 5, 3, pp. 297-332, 1974.

CHAPTER 7

EXTREME PROPERTIES OF ECOLOGICAL SYSTEMS

7.1. Ecological introduction

Just as in other sciences with longer histories (mechanics, optics, etc.), so in mathematical ecology there appeared a trend to formulate the basic regularities of population and community dynamics in the form of some extreme principles. Perhaps the reason is the quest for more concise and elegant description on the one hand, and the perennial teleologicity of our thinking, on the other. Though it is hardly probable that there is a goal the population or community tries to attain, nevertheless our hypothesis (which is purely auxiliary in nature) that such a goal exists may put all the variety of ecological mechanisms in a proper perspective.

The first attempt in this line was apparently the hypothesis of A. Lotka (1922) that ecosystems evolve towards the increase of the total energy flow through the ecosystem, this flow being maximal at equilibrium (of course, with due regard for different restrictions). Lotka went so far as to suggest to call this statement "the fourth law of thermodynamics".

In 1930 R. Fisher formulated the so-called "fundamental theorem of natural selection". For a panmictic Mendel's population, with the heredity determined by one polyallele locus, it was shown that the average fitness of a population in a fixed environment approaches maximum, the rate of this approach being in proportion to a characteristic of genes diversity in the population—the genes variance.

The 1950's, beginning with the works of R. Margalef and R. MacArthur, saw a real information boom in ecology. We have already considered such a community characteristic as the *diversity*, which has been widely measured by informational entropy. In numerous works it was postulated that entropy attains maximum in most stable communities. Later it became clear that this regularity was far from being so general.

After E. Odum had brought his energetic method in experimental and theoretical analysis of ecosystems, a new hypothesis of Margalef (1968) about ecosystem evolution came into being. It states the following.

Let M be the specific total biomass of all species in the community, expressed in one and the same units (say, of energy) per unit area, and let P be the specific production of the community, that is the rate of new biomass production for these species, expressed in the same units per unit area per unit time. Then the ratio $\Pi = P/M$, which is known as *the rate of total energy cycling* in the ecosystem, approaches minimum as the system evolutes. The variable η, which is the inverse of Π, is called ecosystem *efficiency*. Hence the ecosystem evolution is towards the state of maximal efficiency. Margalef also states, that this efficiency can only be attained in systems with high diversity indices.

Lastly, in 1971 H. Odum stated the principle, which is different from that of Lotka in that it requires the maximization of capacity in place of maximization of the energy flow.

All the variables, that appear in formulations of these hypotheses, may be measured in real ecosystems, and hence the hypotheses may be experimentally verified, but only in the case where we know the entire topography of the "energetic" surfaces (capacity, efficiency) in the phase space of the system and the entire topography of its phase trajectories. Then we can correlate different trajectories by energy, capacity, or efficiency.

An easier method is to derive well-known dynamic equations which have once been obtained from absolutely different considerations (for instance, the Volterra equations, obtained with balance correlations and some other plausible assumptions) from an extreme principle. Another approach is also possible, that is, to derive from the dynamic equations the correlations, that may be interpreted as extreme principles.

7.2. Frequency form of Volterra equations

If we switch from species populations to their frequencies $p_i = N_i/N$, $N = \sum_{i=1}^{n} N_i$ in the Volterra equations written in their regular form, the equations for the community dynamics take the form

$$\frac{dp_i}{dt} = p_i\,(w_i - w), \qquad w = \sum_{i=1}^{n} p_i w_i, \qquad \sum_{i=1}^{n} p_i = 1, \tag{7.1}$$

$$\frac{dN}{dt} = Nw, \tag{7.2}$$

where

$$w_i = \varepsilon_i - N \sum_{j=1}^{n} \gamma_{ij} p_j = \sum_{j=1}^{n} (\varepsilon_i - N\gamma_{ij})\, p_j.$$

Notice that formally these equations coincide with the ones of population genetics. There is one difference, however. While in genetic equations the functions w_i have the form $w_i = \sum_j \alpha_{ij} p_j$ ($\alpha_{ij} = \alpha_{ji} =$ const are the coefficients of relative viability) and are independent of N, the total population, in the Volterra equations such a dependency is present. For this reason, unlike the genetic equations, the equation for N cannot be separated from the equations for frequencies, and the system (7.1)-(7.2) is to be considered simultaneously. Besides, the Volterra analogy for coefficients α_{ij} ($\alpha'_{ij} = \varepsilon_i - N\gamma_{ij}$) does not exhibit the symmetry property ($\alpha'_{ij} \neq \alpha'_{ji}$ when $\varepsilon_i \neq \varepsilon_j$).

After denoting

$$\sum_{i=1}^{n} \varepsilon_i p_i = \varepsilon, \qquad \sum_{i=1}^{n} \sum_{j=1}^{n} \gamma_{ij} p_i p_j = \sum_{i=1}^{n} \Gamma_i p_i = \Gamma,$$

equation (7.2) for the total community population may be formally rewritten as a logistic equation

$$\frac{dN}{dt} = N(\varepsilon - \Gamma N), \tag{7.3}$$

where ε and Γ depend only upon the frequencies p_i. Vector $\mathbf{p} = [p_1, \ldots, p_n]$ with coordinates $p_i \geqslant 0$, such that $p_1 + \ldots + p_n = 1$ will be called the community *composition*. Clearly the set of all possible compositions is a simplex Σ^n in the positive orthant of the n-dimensional space.

At equilibrium both the composition and the population, are constant, but the rates of their evolution toward this state may be different. If N is now regarded as a parameter, then the equilibrium composition $\mathbf{p}^*$, defined from

$$w_i^* = w^*, \quad \text{or} \quad \varepsilon_i = N\Gamma_i^* = \varepsilon^* - N\Gamma^*, \tag{7.4}$$

will depend upon N. The question arises of whether this dependency is single-valued, i.e. whether there is only one composition associated with each population value. Moreover, it is not known whether the solution to (7.4), $\mathbf{p}^*$, always belongs to the simplex Σ^n, i.e. gives a composition.

Let $\varepsilon_i - \gamma_{ij} N = \alpha_{ij}$. Then, removing the restriction $\Sigma_{p_i} = 1$ by taking into account that $p_n = 1 - (p_1 + \ldots + p_{n-1})$, the system (7.1) may be rewritten in the form

$$\frac{dp_i}{dt} = p_i \sum_k \left[(\delta_{ik} - p_k) \left(A_k + \sum_j B_{kj} p_j \right) \right], \tag{7.5}$$

where

$i, j, k = 1, \ldots, n-1,$

$A_i = \alpha_{in} - \alpha_{nn}, \qquad B_{ij} = \alpha_{ij} - \alpha_{in} - \alpha_{nj} + \alpha_{nn},$

$$\delta_{ij} = \begin{cases} 1, & i = j \\ 0, & i \neq j. \end{cases}$$

Steady-state compositions $\mathbf{p}^*(N)$ may be found if system (7.5) is solved at $dp_i/dt = 0$. What are the possible solutions to this system? The following cases may occur:

(a) there are n solutions of the form $p_i^* = \delta_{ik}$, $i, k = 1, \ldots, n$;

(b) there is only one solution (*non-trivial* or *positive* composition), which has all p_i^* positive. The latter are found as solutions to the linear system

$$\sum_j B_{ij} p_j^* = -A_i, \qquad i, j = 1, 2, \ldots, n-1. \tag{7.6}$$

The existence and uniqueness of the solution are determined by conditions regular for linear systems. However, the wanted solution is not arbitrary, but such that $\mathbf{p}^* \in \Sigma^n$. This implies additional restrictions on A_i and B_{ij}. Since $p_i^* = B^i/B$, where $B = \det \| B_{ij} \|$ and B^i is the determinant we get from B by substituting the ith column for $[-A_1, \ldots, -A_{n-1}]^T$. Therefore $p_i^* > 0$, if sign $B^i =$ $=$ sign $B \neq 0$.

Suppose we are given an $n \times n$ determinant of the form

$$G^1 = \begin{vmatrix} 1 & \alpha_{12} & \ldots & \alpha_{1n} \\ \cdot & \cdot & \cdot & \cdot \\ 1 & \alpha_{n2} & \ldots & \alpha_{nn} \end{vmatrix}.$$

Subtracting the last row from all the rest, then in the resultant determinant, subtracting the last column from all the rest, but the first, and transposing the first and the last column, we get

$$G^1 = \begin{vmatrix} -A_1 & B_{12} & \ldots & B_{1,n-1} & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ -A_{n-1} & B_{n-1,2} & \ldots & B_{n-1,n-1} & 0 \\ -\alpha_{nn} & \ldots & \ldots & \alpha_{n,n-1} - \alpha_{nn} & 1 \end{vmatrix} = B^1.$$

Likewise, we can prove the equalities

$$G^i = \begin{vmatrix} \alpha_{11} & \ldots & \alpha_{1,i-1} & 1 & \alpha_{1,i+1} & \ldots & \alpha_{1n} \\ \vdots & \ldots & \vdots & \vdots & \vdots & \ldots & \vdots \\ \alpha_{n1} & \ldots & \alpha_{n,i-1} & 1 & \alpha_{n,i+1} & \ldots & \alpha_{nn} \end{vmatrix} = B^i,$$

$$i = 2, \ldots, n-1.$$

It may be also shown that $B = G^1 + G^2 + \ldots + G^{n-1} + G^n$. Thus,

$$p_i^* = G^i / \sum_{j=1}^{n} G^j, \qquad i = 1, \ldots, n-1, n,$$

and if either all $G^i > 0$, or all $G^i < 0$, then $0 < p_i^* < 1$, $p_1^* + \ldots \ldots + p_{n-1}^* + p_n^* = 1$, and for any N the community has a non-trivial equilibrium composition.

If at least one determinant $G^i = 0$, then the appropriate $p_i^* = 0$. But, as one may see from (7.5) even if none of G^i is 0, there exist stationary solutions, for which some $p_i^* = 0$, while the rest are non-zero (in Chapter 6 they were termed *partially positive*). These non-zero p_j^* may then be found from a linear system of the form of (7.6) but with fewer equations, and with a matrix, obtained from $\| B_{ij} \|$ by cancelling out the rows and columns with numbers which belong to non-zero components. In the column of the right-hand sides $[\ldots, -A_i, \ldots]^T$ the terms with these numbers are also cancelled.

The count of all possible partially positive stationary solutions to (7.5) leads us to the conclusion that theoretically this system may have $2^n - 1$ (generally speaking, different) stationary compositions.

It was mentioned above that every population N is to have its own stationary solution $\mathbf{p}^*(N)$ (which turns out to be a composition under definite conditions). But is it a one-to-one correspondence?

One may show that the determinants G^i can be presented as

$$G^i = (-N)^{n-2} \sum_{\substack{s=1 \\ s \neq i}}^{n} g_s^i + (-N)^{n-1} g^i, \tag{7.7}$$

where

$$g_s^i = \begin{vmatrix} \gamma_{11} & \cdots & \gamma_{1,s-1} & \varepsilon_1 & \gamma_{1,s+1} & \cdots & \gamma_{1,i-1} & 1 & \gamma_{1,i+1} & \cdots & \gamma_{1n} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \gamma_{n1} & \cdots & \gamma_{n,s-1} & \varepsilon_n & \gamma_{n,s+1} & \cdots & \gamma_{n,i-1} & 1 & \gamma_{n,i+1} & \cdots & \gamma_{nn} \end{vmatrix},$$

$$g^i = \begin{vmatrix} \gamma_{11} & \cdots & \gamma_{1,i-1} & 1 & \gamma_{1,i+1} & \cdots & \gamma_{1n} \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \gamma_{n1} & \cdots & \gamma_{n,i-1} & 1 & \gamma_{n,i+1} & \cdots & \gamma_{nn} \end{vmatrix}.$$

Since $g_s^i = -g_i^s$, it follows that

$$\sum_{i=1}^{n} \sum_{\substack{s=1 \\ s \neq i}}^{n} g_s^i \equiv 0, \qquad \sum_{i=1}^{n} G^i = (-N)^{n-1} \sum_{i=1}^{n} g_i.$$

Then

$$p_i^*(N) = \Big(g^i - N \sum_{\substack{s=1 \\ s \neq i}}^{n} g_s^i\Big) \Big/ \sum_{j=1}^{n} g^j, \qquad i = 1, \ldots, n, \tag{7.8}$$

and hence, each value of N is associated with one and only one vector $\mathbf{p}^*(N)$, that is, only one equilibrium composition belongs to each total population. As far as (7.8) demonstrates a monotonic relationship for N, the inverse statement is also true and the correspondence between population and composition is one-to-one.

In order that $\mathbf{p}^* \in \Sigma^n$, (7.8) produces restrictions not only on g_s^i and g^i, but on N also. We can say that a non-trivial equilibrium composition exists if and only if the total population of the community satisfies the inequalities:

$$N \sum_{s \neq i} g_s^i < g^i, \qquad i = 1, \ldots, n, \qquad \text{for } \sum_i g^i > 0; \tag{7.9}$$

$$N \sum_{s \neq i} g_s^i > g^i, \qquad i = 1, \ldots, n, \qquad \text{for } \sum_i g^i < 0. \tag{7.9'}$$

For some community classes the existence conditions for a non-trivial composition may be specified more definitely. If, say, matrix $\| \gamma_{ij} \|$ is positive definite (for instance, this is the case for competitive communities of Chapter 6.6) and the community is dissipative, then (7.9) is realized. In fact, expanding the determinant g^i in elements of the ith column, we yield

$$g^i = \sum_{k=1}^{n} \tilde{\gamma}_{ki},$$

where $\tilde{\gamma}_{ki}$ is the cofactor of element γ_{ki}. Then

$$\sum_{i=1}^{n} g^i = \sum_{i,k=1}^{n} \tilde{\gamma}_{ki} = \det \| \gamma_{ij} \| \sum_{i,j=1}^{n} \gamma_{ij}^{(-1)}, \tag{7.10}$$

where $\gamma_{ij}^{(-1)}$ is an element of the matrix, reciprocal to $\| \gamma_{ij} \|$, and the last sum in (7.10) is nothing but the value of the quadratic form, resulting from $\| \gamma_{ij} \|^{-1}$ multiplied by vector $[1, 1, \ldots, 1]$. Since this quadratic form is positive definite (on account of $\| \gamma_{ij} \|$ being positive definite) and $\det \| \gamma_{ij} \| > 0$, the inequality $\sum_i g^i > 0$ is satisfied. With regard to the natural restriction $N > 0$ it then follows from (7.9) that for a non-trivial composition to exist it is necessary and sufficient that the condition be satisfied:

$$N < N_{\text{cr}} = \min_i \{ g^i / \sum_{s \neq i} g_s^i \}. \tag{7.11}$$

If this condition is not satisfied, one or several p_i^* are to become zero.

Let $N \to N^* > 0$ as $t \to \infty$. Then there exists a sequence $\mathbf{p}^*(N)$ such that $\mathbf{p}^*(N) \to \mathbf{p}^*(N^*)$ as $t \to \infty$ and this composition is unique.

The representation of the model equations in their frequency form makes it possible to distinguish two processes from the general

evolutionary process: evolution of composition and evolution of total population. These two processes, though connected, are different to a certain extent. Naturally, the rates of the processes may be different.

For instance, the rate of the composition evolution is low, if $\varepsilon_i \simeq \varepsilon$ and $\Gamma_i \simeq \Gamma$. This case is possible (for any composition) in a community of species, which differ slightly both in ecological-physiological parameters and in characteristics of competitive interactions. In such a community the composition evolves slowly. An example is given by ecologically similar species joined together at one trophic level (a horizontally structured community). In this case $\varepsilon = \sum_{i=1}^{n} \varepsilon_i p_i$ may be regarded as the average coefficient of natural growth (for the whole community), and $\Gamma = \sum_{i=1}^{n} \sum_{j=1}^{n} \gamma_{ij} p_i p_j$ — as the average competition coefficient; the competitive characteristic of the ith species $\Gamma_i = \sum_{j=1}^{n} \gamma_{ij} p_j$ is interpreted as the average competition stress for this species. If the composition evolves slowly the total community population, when far from equilibrium and especially for large ε, may vary fast enough, attaining some intermediate equilibrium $N^* (\mathbf{p}) = \varepsilon (\mathbf{p})/\Gamma (\mathbf{p})$, which depends upon the composition, that is taken to be constant over this time interval. Then over large time intervals the composition evolution may be thought of as the determining process in the general evolutionary process of the community, and may be described by system (7.1) with $N \simeq \varepsilon/\Gamma$, that is,

$$\frac{dp_i}{dt} = p_i \left(\varepsilon_i - \frac{\varepsilon \Gamma_i}{\Gamma}\right), \qquad i = 1, \ldots, n. \tag{7.12}$$

The opposite case, when the rate of composition evolution by far exceeds the variation rate of the total population, is also possible. This is typical, for instance, of predator-prey type communities (in particular, vertically structured communities), where populations of some species may oscillate at a high frequency and amplitude, while the total biomass of the community remains practically unchanged or alters slowly enough. In that case for each N the composition quickly equilibrates to $\mathbf{p}^* (N)$, so that to account for the community evolution over large time intervals it is sufficient to use (7.2) with $\varepsilon = \sum_{i=1}^{n} \varepsilon_i p_i^* (N)$ and $\Gamma = \sum_{i=1}^{n} \sum_{j=1}^{n} \gamma_{ij} p_i^* (N)\, p_j^* (N)$ whereas $p_i^* (N)$ are defined by (7.8). Notice that in predator-prey communities the growth coefficients for predators are expressed in terms of γ_{ij}, and the variable ε cannot be regarded here as the average coefficient of

natural growth for the community as a whole; the predator and the prey species should be put into separate classes.

The first case may be called *quasi-equilibrium in size*, while the second is the *quasi-equilibrium in composition*. On the other hand, when the evolution is considered over small time intervals, in the first case the community composition is almost the same; whereas in the second its total population is almost the same; that is, one may speak about *quasi-stationary* evolutionary processes for the composition and the total population of the community.

7.3. Extreme properties of equilibrium composition in horizontally structured community

Ecosystem dynamics for n species in one trophic level, competing for one or several resources (a horizontally structured community), may be described by a system of Volterra equations with a symmetric competition matrix, and hence by equations (7.1), (7.2) with $\gamma_{ij} = \gamma_{ji}$. Consider the function

$$F = \frac{\varepsilon^2}{4\Gamma} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} \varepsilon_i \varepsilon_j p_i p_j}{4\sum_{i=1}^{n}\sum_{j=1}^{n} \gamma_{ij} p_i p_j}, \qquad p_i \in \Sigma^n, \tag{7.13}$$

which is the ratio of two quadratic forms, and examine its extreme points. The necessary extremum condition, with regard to the restriction $\sum_{i=1}^{n} p_i = 1$, may be written in the form (λ is the Lagrange multiplier)

$$\frac{\partial \widetilde{F}}{\partial p_i} = \frac{\partial F}{\partial p_i} + \lambda = \frac{2\varepsilon_i \varepsilon \Gamma - 2\varepsilon^2 \Gamma_i}{4\Gamma^2} + \lambda = 0, \qquad i = 1, \ldots, n. \tag{7.14}$$

Multiplying through (7.14) by p_i and summing over i we get

$$\frac{\varepsilon}{2\Gamma^2}\left(\Gamma \sum_i \varepsilon_i p_i - \varepsilon \sum_i \Gamma_i p_i\right) + \lambda \sum_i p_i = 0,$$

whence, with regard to the notations for ε and Γ of the previous section, it follows that $\lambda = 0$, therefore the restriction $\sum_i p_i = 1$ is not essential. Then at the extremal point within the simplex Σ^n we have

$$\varepsilon_i \Gamma^* = \varepsilon^* \Gamma_i^*, \qquad i = 1, \ldots, n. \tag{7.15}$$

The extremum of F may not be attained within Σ^n. In this case it must be attained on one of its faces, i.e. on a simplex of less dimensions. Then the appropriate extremal p_i^* equal zero, and the number

of necessary conditions (7.15) will be less than n and equal in dimensionality of this simplex.

On the other hand, the equations of the stationary composition (7.4) with the stationary condition for the total population $N = N^* = \varepsilon^*/\Gamma^*$ yield

$$\varepsilon_i^* - N^*\Gamma_i^* = \varepsilon_i^* - \frac{\varepsilon^*\Gamma_i}{\Gamma^*} = \varepsilon^* - N^*\Gamma^* = 0, \qquad i = 1, \ldots, n,$$

that is, the equations, which coincide with (7.15). If some of p_i^* equal zero, then the number of these equations is appropriately reduced.

From all the foregoing the conclusion may be drawn that the stationary community composition $\mathbf{p}^*$ (N^*), for a stationary total population, is an extremal point for the function F. Moreover, as will be shown in the following section, if this composition is stable, then

$$F(\mathbf{p}^*) = \max_{\mathbf{p}\in\Sigma^n} F(\mathbf{p}).$$

In what way can we interprete this result? And what is the function F? We suggest the following mental experiment. Suppose we have a community, whose composition evolves much more slowly than its total population. Then over small time intervals the community dynamics is characterized accurately enough by the logistic equation (7.3) for the total population, where ε and Γ may be considered constant. Suppose biomass is continuosly taken from this community (the harvesting problem), with the community composition preserved in this process. We organized thus, a flow-through system, and the energy, which was dissipated before, is now gathered as harvest (the energy confined in biomass). Therefore the harvest may serve as a measure of energy that flows through the system. The biomass dynamics in such a system is given by the equation

$$\frac{dN}{dt} = N(\varepsilon - N\Gamma) - f, \tag{7.16}$$

where f is the rate of biomass removal. It can be shown that the maximal removal rate is

$$f^* = \max_N f = \max_N [N(\varepsilon - N\Gamma)] = \frac{\varepsilon^2}{4\Gamma},$$

i.e. $f^* = F$. In this case the community is preserved indefinitely. If $f > f^*$, the biomass (population) of the community will decline, approaching zero in the limit, so suggesting that community dies out. The variable $F = \varepsilon^2/4\Gamma$ may stand for the maximum *capacity* of the community of a given composition. Clearly, the higher the energy flow rate, the more biomass may be removed per unit time,

and the higher the capacity of the community. Therefore F may be regarded as a measure of the energy flow rate. The composition, for which $F(\mathbf{p}^*) = \max\limits_{\mathbf{p}\in\Sigma^n} F$, provides a maximum maximorum for the capacity, i.e. the maximal energy flow rate through the community. And since the community evolves exactly towards this composition, we can say that the extreme principle of H. Odum works here.

Finally, *a community of n species competing for one or several resources, evolves so that to increase its capacity or energy flow rate, this capacity (or rate) being maximal at equilibrium.*

The stated principle tells us nothing about the evolution—whether the energy flow rate increases steadily, or are there parts of trajectories, where the rate, in contrast, declines? The principle also says nothing about the evolution rate. In essence, it is a local principle.

In conclusion we notice that the composition, optimal in this sense, need not comprise all the species—as the case might be where the community evolution results in elimination of some of its species.

7.4. Global extreme properties of trajectories of horizontally structured community

While the principle stated in the preceding section was of a local character (strictly speaking, a steady increase in capacity may only be ensured in a sufficiently small neighborhood of the equilibrium state), the principle, which is to be stated in this section, will be globally valid, that is, for any community trajectory in the positive orthant. The proof is easier for the model in populations, i.e. for the Volterra equations in their classic form

$$\frac{dN_i}{dt} = N_i\left(\varepsilon_i - \sum_{j=1}^{n} \gamma_{ij}N_j\right), \tag{7.17}$$

$$i = 1, \ldots, n, \qquad \varepsilon_i,\ \gamma_{ij} \geqslant 0, \qquad \gamma_{ij} = \gamma_{ji}.$$

Consider the transformation $\eta_i = \pm 2\sqrt{N_i}$ $(i = 1, \ldots, n)$ which transfers the positive orthant P^n into the entire coordinate space R^n_η. It turns out that in R^n_η the trajectories of (7.17) serve as the steepest ascent trajectories for the function

$$W = \frac{1}{4}\sum_{i=1}^{n} \varepsilon_i\eta_i^2 - \frac{1}{32}\sum_{i,\,j=1}^{n}\sum \gamma_{ij}\eta_i^2\eta_j^2$$

$$= \sum_{i=1}^{n} \varepsilon_i N_i - \frac{1}{2}\sum_{i,\,j=1}^{n}\sum \gamma_{ij}N_iN_j, \tag{7.18}$$

therefore, the equation holds

$$\frac{d\eta_i}{dt} = \frac{\partial W}{\partial \eta_i}, \qquad i = 1, \ldots, n, \tag{7.19}$$

$$\frac{dW}{dt} = \sum_{i=1}^{n} \frac{\partial W}{\partial \eta_i} \frac{d\eta_i}{dt} = \sum_{i=1}^{n} \left(\frac{\partial W}{\partial \eta_i}\right)^2. \tag{7.20}$$

Obviously, $dW/dt = 0$ only at points where all $d\eta_i/dt$ are zero, i.e. at stationary points of system (7.19). Notice as well, that all these points meet the necessary conditions of the extremum of function $W(\eta)$. If (7.17) has the maximal number (2^n-1) of all possible stationary points with n, $n-1, \ldots, 1$ non-zero coordinates, then any point which differs from these only in signs of non-zero components, will be stationary for system (7.19). The number of such points is, evidently, equal to

$$2^n + n2^{n-1} + \ldots + C_n^k 2^k + \ldots + 2n = 3^n - 1.$$

Thus, the stationary points of system (7.19) are derived from the stationary points of (7.17) as their symmetric reflections with respect to all sorts of coordinate hyperplanes and the origin, the values of function $W(\eta_1, \ldots, \eta_n)$ being identical in symmetric points.

It follows from (7.20) that the function $W[\eta(t)]$ always grows along the trajectories of (7.19) and attains its local maximum at a stationary point η^* if only η^* is asymptotically stable. In fact, since trajectories of the dynamic system (7.19) are dense throughout some region G with the point η^* inside, for each point η from any neighborhood of η^* there may be found a trajectory $\eta(t) \to \eta^*$, which goes through η. The function W is continuous and steadily increasing, therefore it follows that $W(\eta^*) > W(\eta)$ along the trajectory $\eta(t)$. Hence,

$$W(\eta^*) = \max_t W[\eta(t)] = \max_{\eta \in G} W(\eta). \tag{7.21}$$

And since the inverse transfer from R_η^n to P^n merges all the symmetric prototypes into one image—the stationary point for (7.17)—with the value of W unchanged, a statement, similar to (7.21) should hold for trajectories in P^n.

On the other hand, if the function $W(N_1, \ldots N_n)$ has an isolated maximum at some stationary point $\mathbf{N}^\circ = [N_1^\circ, \ldots, N_n^\circ] \in P^n$ then the state $\mathbf{N}^\circ$ is to be asymptotically stable, since in this case the function

$$L(\mathbf{N}) = W(\mathbf{N}^\circ) - W(\mathbf{N}) \tag{7.22}$$

is a Lyapunov function for system (7.17). This fact is obvious enough, since $L \geqslant 0$ in a domain, which contains $\mathbf{N}$ ($L = 0$ only at $\mathbf{N}^\circ$)

and the derivative along system trajectories is $dL/dt = -dW/dt \leqslant \leqslant 0$ with $dL/dt = 0$ only at the point $\mathbf{N}^\circ$.

The sufficient maximum condition for W is that the quadratic form $\sum_i \sum_j \gamma_{ij} N_i N_j$ is positive definite, and in this case W is strictly concave (convex upwards). And as far as the orthant P^n also represents a convex set, W has a unique isolated maximum in this set (on compact subsets or on the boundary)*. Hence the local maximum of W is at the same time global, and system (7.17) has a unique stable equilibrium. Moreover, since $L(\mathbf{N}) \to \infty$ as $\|\mathbf{N}\| \to \infty$, this equilibrium, by the theorem about stability on the whole**, is stable for any initial trajectory displacement within P^n (globally stable, absolutely stable), thus suggesting that any system trajectory initiated within P^n approaches the equilibrium as $t \to \infty$.

If max W is not attained inside the positive orthant P^n, it will be attained on its boundary, in the appropriate coordinate hyperplanes. This implies that in the evolutional process of the ecosystem one or several species are to be eliminated, since the new equilibrium state is again stable. This may happen, for instance, when some of N_i°, given by equations $\sum_j \gamma_{ij} N_j^\circ = \varepsilon_i$, $i = 1, \ldots, n$ are negative.

The squared rate of approach along trajectories of steepest ascent may be defined as

$$v^2 = \sum_{i=1}^{n} \left(\frac{d\eta_i}{dt}\right)^2 = \sum_{i=1}^{n} \left(\frac{\partial W}{\partial \eta_i}\right)^2 = \frac{dW}{dt} = \sum_{i=1}^{n} N_i \left(\varepsilon_i - \sum_{j=1}^{n} \gamma_{ij} N_j\right)^2.$$

It may be seen from this expression that as we approach the steady state the rate is constantly reduced, though it can be sufficiently high when far from this state.

What is the relationship between W and the function F introduced in the previous section? Calculating the value of W at the stable stationary point and taking into account that $N^* = \varepsilon^*/\Gamma^*$, we get

$$W^* = W(\mathbf{N}^*) = N^* \left(\sum_{i=1}^{n} \varepsilon_i p_i^* - \frac{N^*}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} \gamma_{ij} p_i^* p_j^*\right) = \frac{\varepsilon^{*2}}{2\Gamma^*} = 2F(\mathbf{p}^*),$$

that is, the largest values of these two functions are in proportion.

All these results not only provide support for the foregoing qualitative description of behavior of dissipative Volterra systems, but also admit of a sensible interpretation. The variable $V(\mathbf{N}) =$

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* Cf., for instance, Carr C. R., Howe C. W., *Quantitative decision procedures in management and economics*, McGraw-Hill, New York, 1964.

** Cf., for instance, Barbashin E. A. *Introduction to stability theory*, Nauka, Moscow, p. 46-47, 1967 (in Russian).

$= \sum_{i=1}^{n} \varepsilon_i N_i$ in essence, accounts for the rate of biomass gain in case competition and any kind of limitation by resource are absent, and the growth is only determined by the physiological fertility of the organisms and by their natural mortality. Therefore it is only natural to term V *reproductive potential* of the community. The analog of this notion found in the literature is the *total production* of the ecosystem. The expression $G = \frac{1}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} \gamma_{ij} N_i N_j$ may be used to measure the rate of energy dispersion resulting from inter- and intraspecific competition, i.e. the total community biomass consumption for competition. Therefore we shall refer to G as *total expenses in competition*, or, again in purely ecological language, ecosystem *respiration losses*. Hence the increase in W in the process of evolution may be visualized as the tendency of the community to maximize the difference between its reproductive potential and the total expenses in competition. This can be done in several ways: either the reproductive potential is maximized at fixed expenses in competition, or the competition expenses are minimized for a bounded reproduction potential (there may be some intermediate cases) as well. Observational evidence indicates that in nature all the cases are realized. Consider, for instance, the so-called *r-competition* and *K-competition*, which refer to two opposite mechanisms of population regulating.

The origin of these terms becomes clear, if we turn to a somewhat different form of equations (7.17) (cf. Section 6.2):

$$\frac{d\tilde{N}_i}{dt} = \frac{r_i \tilde{N}_i}{K_i} \left(K_i - \sum_{j=1}^{n} \alpha_{ij} \tilde{N}_j \right), \qquad i = 1, \ldots, n, \tag{7.23}$$

where

$$r_i = \varepsilon_i, \qquad \alpha_{ij} = \gamma_{ij} \frac{K_i K_j}{r_i r_j}, \qquad \tilde{N}_i = N_i \frac{r_i}{K_i}.$$

Evidently, a scaling change of variables does not alter the structure of the phase space, and all the properties of solutions to (7.17) remain valid for solutions to (7.23), since $\alpha_{ij} = \alpha_{ji}$, when $\gamma_{ij} = \gamma_{ji}$.

Since $r_i = \varepsilon_i$ is nothing but the natural growth coefficient of the ith species, the species which win out in competition by increasing their own fertility are said to utilize the *r-strategy*. And since K_i is the environment capacity for the ith species, the species which win out in competition by optimizing the resource consumption (uptake of a wide resource spectrum, reduction of competition expenses by means of a "wise" resource distribution, etc.) are said to utilize the *K-strategy*. Thus, it may be said that the *r-strategy* of the community implies maximization of the reproduction potential, whereas the *K-strategy* is the minimization of total competition expenses

And in conclusion, we give another interpretation for the statement proved in the previous section, that the function F (p) attains a maximum at equilibrium. Let the community evolutional process be quasi-stationary with respect to total population, i.e. the quasi-equilibrium of population $N(t) \approx \varepsilon\,[\mathbf{p}\,(t)]/\Gamma\,[\mathbf{p}\,(t)]$ is attained rather quickly when the evolution of the composition is slow. Then

$$F(\mathbf{p}) = \frac{\varepsilon^2}{4\Gamma} = \frac{1}{4}\,\varepsilon N = \frac{1}{4}\sum_{i=1}^{n} \varepsilon_i N_i = \frac{1}{4}\,V.$$

It follows that *the community evolves towards a state with the composition, which brings a maximum to its reproduction potential.* However, this is a local principle.

7.5. Some interpretations for extreme properties of horizontally structured communities. MacArthur's principle of close packing

If there may exist a non-trivial equilibrium $[N_i^*, \ldots, N_n^*]$ in the community, it should satisfy the system $\varepsilon_i = \sum_{j=1}^{n} \gamma_{ij} N_j^*$, $i = 1, \ldots$ $\ldots, n$. Then, substituting the sum $\sum_{j=1}^{n} \gamma_{ij} N_j^*$ for ε_i in the expression for W, the latter may be represented in the form:

$$W = -\frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{n} \gamma_{ij}\,[N_i N_j - (N_i^* N_j + N_i N_j^*)]$$

$$= -\frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{n} \gamma_{ij}\,(N_i - N_i^*)\,(N_j - N_j^*) + W^*, \qquad (7.24)$$

whence

$$L = W^* - W = \frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{n} \gamma_{ij}\,(N_i - N_i^*)\,(N_j - N_j^*). \qquad (7.24')$$

Since W grows along the trajectory, L is also to increase when going further from the stable equilibrium. This may be regarded as a peculiar form of the *Le Chatelier principle*: any displacement from the stable equilibrium increases the competition expenses in the community.

Let the equations of the community be given in the form of (7.21). As shown in Section 6.2, these equations may be interpreted in terms of the ecological niche, which, in turn, are related to the concept of the ecological or living space. Up till now the definition of

the ecological niche relied on the notion of the resource, so that $K(x)$ (resource spectrum) was visualized as the amouns of resource of the "size" x potentially available for the community whereas $f_i(x)$ (utilization function) was looked upon as the probability density for the uptake of resource of the size x by specimens the ith species. Consequently the coefficients of system (7.21) may be expressed in terms of $K(x)$ and $f_i(x)$ by formulas (6.5) and (6.6) of Chapter 6.

If we now take some living space as the resource (covering by this notion all the environmental factors that are vitally important for specimens in the community; e.g. food, habitat, temperature, etc.), then $K(\mathbf{x})$ may be regarded as the really existing volume of the living space (for a given state of environment $\mathbf{x}$) and $f_i(\mathbf{x})$, as the elementary volume in this space, needed for one specimen of ith species to live in (at the same state of environment x). Then the function

$$\mathscr{D}(\tilde{N}_1, \ldots, \tilde{N}_n) = \int \left[K(\mathbf{x}) - \sum_{j=1}^{n} f_i(\mathbf{x})\, \tilde{N}_i\right]^2 d\mathbf{x}, \tag{7.25}$$

where the integral is taken over the entire space of invironmental factors, may be interpreted as the mean square difference between the really existing and required living spaces (for a community with species populations $\tilde{N}_1, \ldots, \tilde{N}_n$). If every species is considered to occupy a certain volume in this space, then the function $\mathscr{D}$ may be taken to be the *measure of how closely* the species are packed in the given environment, and the less the $\mathscr{D}$, the closer the species are packed.

We now prove that in the equilibrium state $\mathbf{N}^\circ$ the function $\mathscr{D}(N_1, \ldots, N_n)$ attains a minimum, which is global for the positive orthant P^n, and what is more, along all the community trajectories $d\mathscr{D}/dt \leqslant 0$, with $d\mathscr{D}/dt = 0$ only at the equilibrium point. Using the expressions for K_i and α_{ij} in terms of $K(\mathbf{x})$ and $f_i(\mathbf{x})$—formulas (6.5) and (6.6)—the function $\mathscr{D}$ may be written in the form

$$\mathscr{D} = \int K^2(\mathbf{x})\, d\mathbf{x} - 2\sum_{i=1}^{n} K_i \tilde{N}_i + \sum_{i,j=1}^{n}\sum \alpha_{ij} \tilde{N}_i \tilde{N}_j \tag{7.26}$$

(supposing that the integral is convergent). Denote in (7.26) the first term, which is independent both of x and i, by $\mathscr{D}_0$. If we now recall that $\alpha_{ij} = \gamma_{ij}(K_i K_j)/(r_i r_j)$ and $r_i = \varepsilon_i$, and return to the original variables $N_i = \tilde{N}_i K_i / r_i$, we can write

$$\mathscr{D} = \mathscr{D}_0 - 2\sum_{i=1}^{n} \varepsilon_i N_i + \sum_{i=1}^{n}\sum_{j=1}^{n} \gamma_{ij} N_i N_j = \mathscr{D}_0 - 2W, \tag{7.27}$$

where $W(N_1, \ldots, N_n)$ is the function introduced in Section 7.4. Since W always grows along the trajectories leading to stable equilib-

rium, and attains an isolated maximum in this state, function $\mathscr{D}$ is to fall off along these trajectories, reaching a minimum at the equilibrium point.

Clearly, the extremal points of $\mathscr{D}$ coincide with the extremal points of W and, thus, they may be found among the equilibrium points of system (7.17) or (7.23). That the competition matrix $\| \alpha_{ij} \|$ is positive definite, which obviously implies that $\| \gamma_{ij} \|$ is positive definite, indicates that the function $\mathscr{D}$ has a unique minimum within the positive orthant P^n (on its compact subsets or on the boundary), this minimum coincides with the only stable equilibrium point, and $\mathscr{D}$ declines along all the trajectories beginning in P^n.

Thus, if there is a positive equilibrium $\mathbf{N}^*$ in the system, operating in an ecological space with the "volume" K (x), then it should be stable, i.e. all the n community species are preserved and function $\mathscr{D}$ attains a minimum on P^n at the point $\mathbf{N}^*$. If there is no such equilibrium, then the one of the partially stable equilibriums $\mathbf{N}^\circ$, which supplies $\mathscr{D}$ by a minimum on P^n, proves to be stable and the species associated by the zero coordinates vanish from the community.

By examining the function $\mathscr{D}$ we formally determine the largest number of new species, which may be established within the community after an invasion of a small number of individuals belonging to these species. If we suppose that the new species do not alter the characteristics of the ecological space [the function K (x)], then we are to consider an expanding sequence of phase spaces for systems of increasing dimensionality, i.e. the sequence of orthants

$$P^n \subset P^{n+1} \subset P^{n+2} \subset \ldots,$$

and the associated sequence of minimal values for the function $\mathscr{D}$ (N)

$$\min_{\mathbf{N} \in P^n} \mathscr{D}(\mathbf{N}) \geqslant \min_{\mathbf{N} \in P^{n+1}} \mathscr{D}(\mathbf{N}) \geqslant \min_{\mathbf{N} \in P^{n+2}} \mathscr{D}(\mathbf{N}) \geqslant \ldots . \tag{7.28}$$

By the definition of (7.25) $\mathscr{D}$ (N) is never negative, and so the sequence (7.28) is bounded below and, accordingly, by the Weierstrass lemma it has a limit which is greater than or equal to zero. If this limit is attained by a member of the sequence with a finite number, then the dimensionality of the corresponding orthant is just the largest possible number of species in the community. In particular, this is the case, for instance, when the function K (x) is such that for some

$$K(\mathbf{x}) = \sum_{i=1}^{n} k_i f_i(\mathbf{x}),$$

where all $k_i > 0$. It is readily seen that in this case $[k_1, \ldots, k_n]$ represents a non-trivial equilibrium point and $\mathscr{D}(k_1, \ldots, k_n) = 0$.

Theoretically it is, of course, possible [for some very specific

constructions of K (x) and f_i (x)] that the sequence (7.28) is extended indefinitely. In the light of the results of Chapter 6 this may suggest, for instance, that there exists a positive equilibrium for a system with any number of dimensions n and a given spectrum K (x), since in this case this equilibrium is the only stable one and it provides a minimum to the function $\mathscr{D}$ (N). This may be observed referring to the example of the competition pattern (6.28) with the form of K (x) such that $K_i = K$ const > 0 for all i.

The results obtained above may be stated as the following principle: *a community of species, competing for the living space, evolves towards the most closely packed state (the minimum of $\mathscr{D}$) so that the species packing becomes more and more close in the evolutional process, attaining the maximal possible value for the given environment at the equilibrium state.*

As $\mathscr{D}$ is minimal at a stable equilibrium, this indicates that there is no free living space in the community, needed, for instance, for introduction and establishment of a new species with characteristics similar to those of a species already present in the community. Such an introduction becomes possible only if the new species uptakes the types of resources (or occupies the regions of the living space determined by the environment), which were left without use by the original species. But from the viewpoint of our formal scheme this already implies an alteration of properties of the ecological space, i.e. the change in the form of the function K (x) and, accordingly, of the function $\mathscr{D}$ (N_1, . . ., N_n).

Similar concepts were repeatedly suggested in the works of such a leading ecologist as R. MacArthur, and therefore, it is only natural to refer to the above formulated principle of close packing as the *MacArthur principle.*

Summerizing we notice that the most close packing may also be attained when one or several species are eliminated from the community. In this case the function $\mathscr{D}$ is to have a minimum in one of the coordinate hyperplanes.

7.6. Extreme properties of general-type Volterra systems

Consider now a Volterra community, represented by system (7.17) where ε_i may have any sign, and there are no restrictions on coefficients γ_{ij}. Suppose there exists a non-trivial positive solution to the system

$$\sum_{j=1}^{n} \gamma_{ij} N_j^* = \varepsilon_i,$$

that is a non-trivial community equilibrium.

Consider the function

$$L = \sum_{i=1}^{n} \left\{(N_i - N_i^*) - N_i^* \ln \frac{N_i}{N_i^*}\right\}. \tag{7.29}$$

Since $N_i/N_i^* - 1 \geqslant \ln (N_i/N_i)$ for any $N_i^* \geqslant 0$ (the identity taking place only for $N_i = N_i^*$), L is positive everywhere in the positive orthant P^n, vanishing only at the steady-state point. If we now change to the variables $\xi_i = \ln (N_i/N_i^*)$, the Volterra system takes the form

$$\frac{d\xi_i}{dt} = -\sum_{j=1}^{n} \gamma_{ij} \frac{\partial L}{\partial \xi_j}, \qquad i = 1, \ldots, n. \tag{7.30}$$

Notice that system (7.30) is most easily reducible to the regular Hamilton form, but for what follows the form of (7.30) is sufficient. Calculating dL/dt along the trajectories of (7.30) we get

$$\frac{dL}{dt} = \sum_{i=1}^{n} \frac{dL}{d\xi_i} \frac{d\xi_i}{dt} = -\sum_{i=1}^{n} \sum_{j=1}^{n} \gamma_{ij} \frac{\partial L}{\partial \xi_i} \frac{\partial L}{\partial \xi_j}. \tag{7.31}$$

Regarding L as the Lyapunov function for the Volterra system, one can readily say that if the quadratic form $\sum_i \sum_j \gamma_{ij} x_i x_j$ is positive definite, then the non-trivial community equilibrium is asymptotically stable, if it is negative definite, then the equilibrium is unstable. In the classic Volterra predator-prey model (when $\gamma_{ij} = -\gamma_{ji}$) $\sum_{i=1}^{n} \sum_{j=1}^{n} \gamma_{ij} x_i x_j \equiv 0$ and the equilibrium is stable, but not asymptotically. Thus, the sign in (7.31) plays a decisive role in deciding whether the non-trivial community equilibrium is stable or unstable. This fact can be given the following meaningful interpretation.

The quantity $N = \sum_{i=1}^{n} N_i$ is nothing but the overall population or the total biomass of the community, and the term $S = \sum_{j=1}^{n} N_i^* \ln (N_i/N_i^*)$ resembles by its structure the informational entropy. In analogy with the diversity measure D frequently used in ecology (cf. Introduction) we shall call it the *equilibrium diversity* of a community. What are the properties of this variable? It is easily seen that at equilibrium $S^* = 0$. Let the community evolution be such that its total biomass stays constant and only the composition is changed. Then $N = N^* = \text{const}$, and $S < 0$ for any $N_i \neq N_i^*$. The latter follows from the fact that $L = -S > 0$ in this case.

Thus, it may be said, that the equilibrium diversity of the community is maximal at the non-trivial equilibrium state.

Then it follows from the condition that dL/dt is negative (one of the sufficient stability conditions), that if the inequality

$$\frac{dS}{dt} \geqslant \frac{dN}{dt} \tag{7.32}$$

is satisfied along a trajectory leading towards a non-trivial equilibrium, then this equilibrium is stable. (The identity is to take place only on the singular trajectory—at the stationary point itself.) The inequality (7.32) may be interpreted in the following way: *when a community evolves towards a stable non-trivial equilibrium, its equilibrium diversity increases at a rate which is to be at least no less than the rate of the total biomass growth.* If the inequality (7.32) is reversed, this indicates that the equilibrium is unstable, and the community evolution is to result in extinction of one or several species, i.e. the community begins to disintegrate. In order to sustain the original number of species under the reduction of the total biomass it is sufficient that this reduction surpass the decrease in the equilibrium diversity.

Finally, let us have a look at how the above-stated stability conditions are related to the spectrum of eigenvalues of the matrix $\Gamma = \| \gamma_{ij} \|$. The first sufficient condition of asymptotic stability for the equilibrium $N^* > 0$ resides in the requirement (cf. Section 4.5) that all the real parts of eigenvalues for the matrix $\| N_i^* \gamma_{ij} \|$ are to be positive, and thus the stability is dependent not only upon the properties of the community matrix Γ, but also on the equilibrium values N_i^*. Recall that for one fairly broad class of matrices, namely the normal matrices ($\Gamma\Gamma^T = \Gamma^T\Gamma$), all the stability properties appearing in the diagram (4.32) are equivalent. In particular, this means that a stable matrix $(-\Gamma)$ (all $\mathrm{Re}\ \lambda < 0$) is associated with a D-stable community, which is stable for any values of $N_i^* > 0$. Symmetric ($\gamma_{ij} = \gamma_{ji}$) and screw-symmetric ($\gamma_{ij} = -\gamma_{ji}$) matrices are special cases of normal matrices, yet they belong to classic Volterra models. For these matrices it immediately follows from the positiveness of $\mathrm{Re}\ \lambda\ (\Gamma)$, that the form $(\Gamma \mathbf{x}, \mathbf{x})$ is positive definite and thereby the non-trivial equilibrium is stable [say, by condition (7.32)]. In this case it is sufficient to check whether or not (7.32) is satisfied for only a certain part of the trajectory. The failure of inequality (7.32) somewhere on the trajectory indicates that the form $(\Gamma \mathbf{x}, \mathbf{x})$ is not positive definite, i.e. there are numbers in the spectrum of Γ such that $\mathrm{Re}\ \lambda\ (\Gamma) \leqslant 0$. And this in turn means that the normal matrix $(-\Gamma)$ cannot be D-stable, and therefore the community may be unstable according to the values of N_i^*.

We can be absolutely sure that instability is the case only when the condition opposite to (7.32) holds everywhere on the trajectories,

and then this is true of arbitrary matrices Γ. Thus, the role of local community behavior in the analysis of its behavior on the whole becomes clear.

7.7. Principle of maximum diversity and community trophic structure

Up till now in this chapter we dealt with dynamic models in the form of some systems of differential equations. Unfortunately, following these lines of modeling we failed to obtain an extreme principle like the maximum diversity principle of the Margalef type. Therefore, it might be reasonable to return to a qualitative description of the community in terms of a trophic graph. On the other hand, as it has been already demonstrated in the Introduction, the classical diversity measure like the informational entropy in no way accounts for the really existing hierarchical community structure, and apparently needs a modification of some kind.

Suppose we have a community with its trophic structure represented by a trophic graph. The vertices are associated with species, and the directed links represent the predator-prey type interactions between these species. If we take into account the input of the external resource to the system (for instance, the solar energy for the producing species), we obtain additional links between the resource and these species. Graphs of this kind, much simplified as compared with the graphs of real communities, but still keeping the basic principal features of these structures, are exampled in Fig. 46.

In each graph one may find linear structures, known as trophic chains or vertically structured communities. In a chain every species is connected with only two other species (the preceding and the succeding ones), or only with the preceding species, if the chain terminates in the given species. In a sufficiently complex community one and the same species may belong to several chains. For instance, communities illustrated in Fig. 46*c*, *d* display two chains each: (*c*) $R \to 1 \to 3$ and $R \to 2 \to 3$; (*d*) $R \to 1 \to 2$ and $R \to 1 \to 3$. Species *3* in Fig. 46*c* and species *1* in Fig. 46*d* belong to both chains.

Define the number I_i^j—the *trophic index* of the *i*th species in the *j*th chain—as the overall amount of links between all the vertices in the chain, preceding the *i*th one (beginning from the vertex R up to the vertex i). For instance, the index of species *3* in the chain $R \to 1 \to 3$ equals 2, whereas the index of species *1* in the same chain is 1 (cf. Fig. 46*c*). (The vertices preceding for the given one are those which may be reached when moving along the trophic chain in the direction opposite to that of the links.) If a certain *i*th species belongs to several trophic chains, then the general *trophic index* for this species is $I_i = \Sigma I_i^j$, where the sum is taken over all the chains involv-

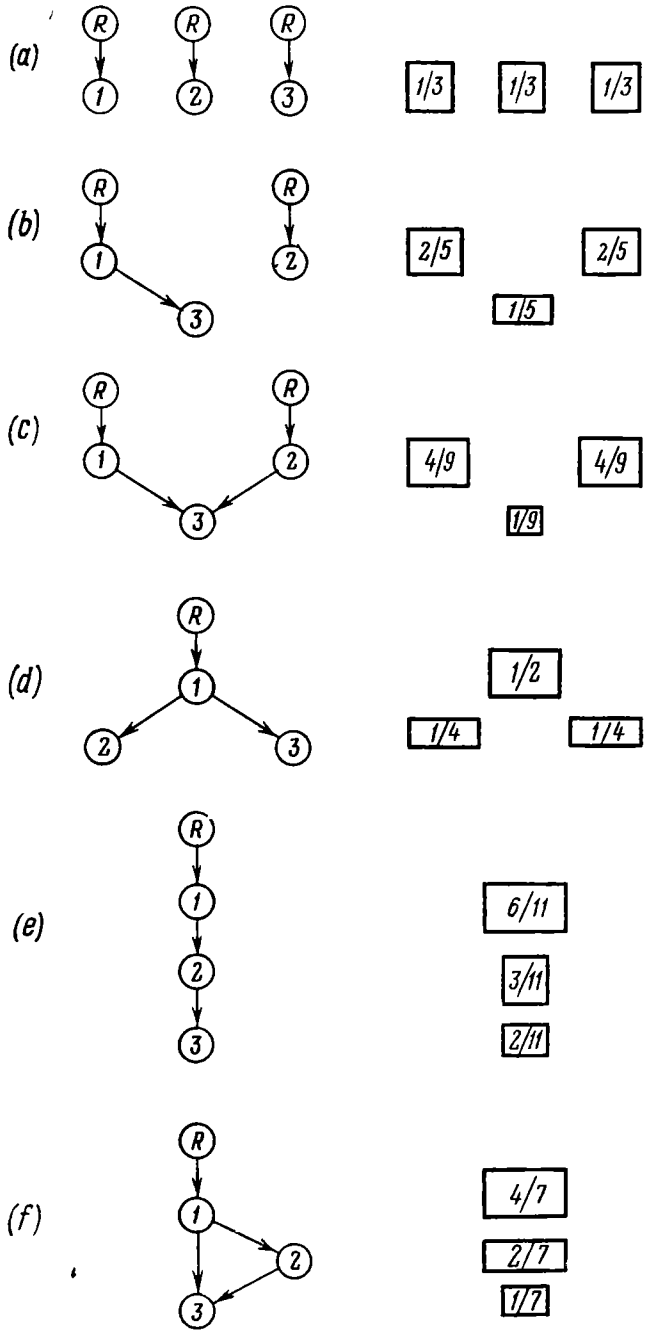

Fig. 46. Examples of trophic graphs and the appropriate diagrams of frequency distributions, maximizing the measure of "trophic diversity" in (7.35).

ing this ith species. For instance, in Fig. 46*c* $I_3 = 4$ while in Fig. 46*d* $I_1 = 1$.

If now the ith species population in the community is N_i, and its frequency is $p_i = N_i/\sum_i N_i$, then the *complexity* of the ecosystem (the community) may be defined as

$$I = \sum_i p_i I_i. \tag{7.33}$$

The notion of the *trophic frequency* of ith species is defined in terms of complexity and the trophic index:

$$\varphi_i = \frac{p_i I_i}{I}, \qquad \sum_i \varphi_i = 1, \qquad \varphi_i \geqslant 0. \tag{7.34}$$

This notion takes into account not only the abundance of a given species, but also its role in the trophic structure and in the community hierarchy. Finally, by analogy with the classic Margalef definition for the diversity measure, we shall define this measure as

$$D = -\sum_i \varphi_i \ln \varphi_i. \tag{7.35}$$

If we now postulate that the diversity is maximal at the equilibrium state, what are the equilibrium compositions we are to obtain? Examples of graphs from Fig. 46*a-f* are used to illustrate this. Clearly, the $\max_{\varphi_i} D$ is attained for $\varphi_1 = \varphi_2 = \varphi_3 = 1/3$. Calculate the trophic indices for all the three species in all the three cases: (*a*) $I_1 = I_2 = I_3 = 1$; (*b*) $I_1 = I_2 = 1$, $I_3 = 2$; (*c*) $I_1 = I_2 = 1$, $I_3 = 4$; (*d*) $I_1 = 1$, $I_2 = I_3 = 2$; (*e*) $I_1 = 1$, $I_2 = 2$, $I_3 = 3$; (*f*) $I_1 = 1$, $I_2 = 2$, $I_3 = 4$. Next, by formulas (7.33) and (7.34) one may easily find the optimal values of p_i^*. They are depicted as diagrams in Fig. 46, the area of rectangles is in proportion to p_i^*. We see that the resulting figures resemble the pyramids of populations or biomasses really observed in most natural ecosystems. Hence it is hoped that this description also reflects some of the really existing regularities, and that it may be useful for prime analysis of ecosystem properties such as complexity and diversity. But it is obviously insufficient for stability analysis, just as the community diversity alone clearly is not sufficient to characterize such a dynamic ecosystem property as stability.

7.8. Conclusion

Concluding this chapter we have a certain feeling of dissatisfaction. Though in some special cases we managed to look at the results of stability analysis of dynamic models of communities from the viewpoint of extreme principles, however, we are still very far away

from the lucidity achieved, say, in classical mechanics. Apparently, the reason is that in mathematical ecology we are still at the stage of phenomenological description of the laws governing species interactions. Whereas in mechanics we have Newton's laws to derive equations of motion from the general conservation laws, in ecology we have no such laws (or, to be more accurate, their analogs). What are the energy expenses in competition? What is the relation between energy utilized in reproduction and energy consumed for the individual specimen life? The list of these questions may be continued. Clearly, so long as we do not know the mechanisms governing the processes of interaction between specimens in the ecosystem and the quantitative expressions for them, all the attempts to moving global energetic properties of the ecosystem to its local behavior will be speculative. Notice that this is the case not only in mathematical ecology, but, say, in mathematical economics too. Attempts to introduce some global energetic characteristics there also did not pay off.

7.9. Notes and bibliography

To 7.1. Discussions of the role of teleological principles in biology and about their acceptability date from very long ago and now they are as heated as before. A new outburst in the discussion occurred about 10 years ago, when the so-called "systems analysis" came into play (though it did not develop from nonentity—"systems theory" has its own venerable history). We shall quote just one statement ascribed to von Brükke, in which teleology is characterized as "a lady no biologist can live without, but whose company seems shameful in society" (Cited from:

Davis B. D., "The teleonomic significance of biosynthetic control mechanisms" N.Y. Biol. Ass., 1961 (*Cold Spring Harbor Symposium on Quantitative Biology*; Vol. 26).

A. Lotka stated his principle for the first time in the papers:

Lotka A. J., "Contribution to the energetics of evolution," *Proc. Nat. Acad. Sci. USA*, 8, 6, pp. 147-151, 1922;

Lotka A. J., "Natural selection as a physical principle," *Proc. Nat. Acad. Sci USA*, 8, 6, pp. 151-154, 1922

this principle, however, is presented in more detail in the book:

Lotka A. J., *Elements of mathematical biology*, Dower, New York, 1956.

For the "fundamental theorem of Fisher" see

Fisher R. A., *The genetical theory of natural selection*, Clarendon Press, Oxford, 1930.

The theorem is analyzed and possibilities of its generalization are considered in the paper:

Svirezhev Yu. M., "Possible ways of generalization for the Fisher fundamental theorem of natural selection," *Zhurnal Obshchei Biologhii*, 35, 4, pp. 590-601, 1974 (in Russian).

Informational entropy measures of stability were first suggested in the works:

MacArthur R. H., "Fluctuations of animal population, and a measure of community stability," *Ecology*, 36, 3, pp. 533-536, 1955;

Margalef R. A., "A practical proposal to stability," *Publ de Inst. de Biol. Apl. Univ. de Barcelona*, 6, 1, pp. 5-19, 1951.

How the concepts of Margalef were further developed is most fully described in the book:

Margalef R., *Perspectives in ecological theory*. Chicago, Univ. Chicago Press, 1968.

The Margalef diversity became most widespread in hydrobiological work. In the last decades hundreds of works have appeared that are basically concerned with measurements of the diversity D in different water ecosystems. Apparently this may be explained by the fact that Margalef himself is a hydrobiologist. But, as is often the case, his successors are "even more orthodox royalists than the king himself" and they anticipated Margalef by far in making this parameter "absolute".

The principle of H. Odum is stated in his book:

Odum E. T., *Environment, power and society*, Wiley (Interscience), New York, 1971.

In this book, in addition to the principle, H. Odum attempts to construct a general language for describing ecological, economical and social processes and introduces a common energetic equivalent to compare biological and social phenomena, which are most frequently very hard to compare. Despite being controversial, the book is very interesting.

To 7.2. Equations of mathematical genetics may be found in the above-cited book by R. Fisher. Another book may be also recommended:

Dynamic theory of biological populations, Ed. R. A. Poluektov, Nauka, Moscow, 1974 (in Russian).

Usually equations of mathematical genetics are written in the frequency form, while equations of the theory of biological communities are in terms of populations of composing species. First the equations describing the evolution of genotype numbers in the population, were derived by V. A. Kostitzin in the book:

Kostitzin V. A. *La biologie mathématique*, A. Colin P., 1937.

It was suggested to use the frequency form of the Volterra equations in the work:

Svirezhev Yu. M., *Mathematical models in populational genetics*. Author's abstract of the doctor's thesis, Pushino, Inst. Biophysics, Acad. Sci. USSR, 1972 (in Russian).

To 7.3. For the problems of optimal harvesting in populations and communities, see:

Svirezhev Yu. M., Yelizarov E. Ya., *Mathematical modelling for biological systems*, Nauka, Moscow, 1972 (in Russian).

To 7.4. The idea to use the substitution $\eta = \pm 2\sqrt{N_i}$, as well as the extreme principle for the function $W = \sum_{i=1}^{n} \varepsilon_i N_i - \frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{n} \gamma_{ij} N_i N_j$ were proposed in the above-cited book by Svirezhev and Yelizarov. There it was also shown that the function $L(\mathrm{N}) = W(\mathrm{N}^*) - W(\mathrm{N})$ is a Lyapunov function for the system of equations characterizing the dynamics in a competitive community.

Notions of the r-competition and K-competition (as well as the r-strategy and K-strategy, respectively) seem to be first formulated clearly in the book:

MacArthur R. H., Connell J. H., *The biology of populations*, J. Wiley, New York, 1966.

To 7.5. The principle of close packing as an extreme principle for the function

$$\mathscr{D}(N_1, \ldots, N_n) = \int \left[K(x) - \sum_{j=1}^{n} f_i(x) N_i \right]^2 dx$$

was stated by R. MacArthur in his two papers:

MacArthur R. H., "Species packing and what interspecies competition minimizes," *Proc. Nat. Acad. Sci. USA*, 64, 4, pp. 1369-1375, 1969; MacArthur R. H., "Species packing and competitive equilibrium for many species," *Theor. Pop. Biol.* 1, 1, pp. 1-11, 1970.

To 7.6. Most of the results in this section are derived in the book by Svirezhev and Yelizarov mentioned above, and also in the postscript written by Yu. M. Svirezhev for the Russian translation of the book by V. Volterra. Some interpretations of the results (among them some of a global character) may be found in the paper:

Svirezhev Yu. M., "Systems analysis of the biosphere: the present state of concepts of the classic Russian school," Nauka, Moscow, 1977, pp. 225-236. (*Problems of cybernetics*; Vol. 32) (in Russian).

To 7.7. The idea to measure the community diversity in this way is presented in the paper:

Tansky M., "Structure, stability and efficiency of ecosystem." In: *Progress in Theoretical Biology*, Academic Press, New York, Vol. 4, pp. 205-262, 1976,

from where the examples of trophic graphs, illustrated in Fig. 46 are taken.

CHAPTER 8

STABILITY OF SPATIALLY DISTRIBUTED ECOSYSTEMS

8.1. Ecological introduction

So far we have been dealing with models of ecosystems uniformly distributed in space. It was taken as granted that their characteristics where common for all points in space and therefore a local description at the point was regarded as sufficient for a general description of the ecosystem. However, in systems with sharp disturbances of homogeneity such a description will be incorrect. Examples are provided by oceanic ecosystems, where the amount of the main resource—the sunlight—essentially varies with depth for purely physical reasons. This factor predetermines the heterogeneity in the depth distribution of basic producing species (phytoplankton) and consequently, the spatial heterogeneity of the oceanic ecosystem on the whole. Another example: non-homogeneous distribution of a food resource throughout the areal results in mosaic patterns of the community spatial distribution. All the community falls into smaller subcommunities (composed of the same species), linked together by migration flows. Lastly, any specimen has a certain radius of individual activity and moves in space. And if specimens of different species have different radii of individual activity, the community necessarily demonstrates spatial heterogeneity in the distribution of species populations over the areal.

As a result of spatial redistribution of specimens and populations equilibria of a very peculiar kind may appear, the so-called spatially equilibrium patterns. At the same time this process may cause a loss in stability in local equilibria.

Finally, we remark that purely ecological processes which give rise to spatially isolated communities, serve as trigger mecanisms of macroevolution, since isolation represents one of the necessary conditions of species formation.

Thus, spatial heterogeneity in populations and communities and the migration processes are of great interest both from the ecological and genetic viewpoints. While geneticists examine the influence of these factors on the genetic structure of the population, ecologists are interested in the role of spatial heterogeneity and migration in ecosystem stabilization.

8.2. Model of phytoplankton vertical distribution in the ocean

Two basic factors govern the growth dynamics of phytoplankton in the ocean: the intensity of solar radiation decreasing with depth, and the biogenic nutrients coming from the bottom (with upwelling or diffusion flows). Generally the curves of the observed vertical distributions for phytoplankton biomass in the ocean exhibit one or several maxima, with the further steady decrease of biomass with depth. The presence of these maxima is usually explained by non-homogeneity in depth of various abiotic factors: illumination, temperature, and so forth. In our model we shall examine the very simplified case where only illumination varies, declining exponentially with depth. Phytoplankton, being motionless itself, interacts with the flow of nutrients.

Instead of considering a model with distributed parameters, suppose the ecosystem is built of n blocks linked together by equations of continuity. Within each block all the parameters are the same, and a feeding substrate (dissolved nutrients) flow through these blocks at a constant rate, or at a rate depending upon the gradient of concentrations of the nutrients. The flow-chart of this model is illustrated in Fig. 47.

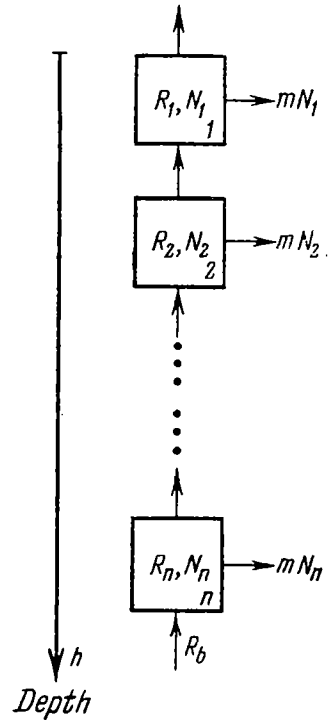

Fig. 47. A model diagram of n blocks describing the interaction between phytoplankton and nutrients in the ocean. Numbers of blocks grow with depth; concentration of nutrients at the bottom is R_b.

Model equations have the form:

(a) *model with a flow*

$$\frac{dR_i}{dt} = q(R_{i+1} - R_i) - \alpha_i R_i N_i,$$

$$\frac{dN_i}{dt} = N_i(k\alpha_i R_i - m), \qquad i = 1, \ldots, n; \tag{8.1}$$

$$R_{n+1} = R_b.$$

(b) *model with diffusion*

$$\frac{dR_i}{dt} = D(R_{i+1} - 2R_i + R_{i-1}) - \alpha_i R_i N_i,$$

$$\frac{dN_i}{dt} = N_i(k\alpha_i R_i - m), \qquad i = 1, \ldots, n, \tag{8.1'}$$

$$R_{n+1} = R_b, \qquad R_0 = 0.$$

Here R_i and N_i are the concentrations of nutrients and phytoplankton biomass, respectively, in the ith block, R_b is the concentration of nutrients at the bottom, q is the upwelling rate (*flow-rate*), D is the diffusion coefficient. The term of the form $\alpha_i R_i N_i$ on the right-hand

sides of the equations appears as a result of the assumption that nutrient uptake by phytoplankton is described by the linear equation, that is, $V_i(R_i) = \alpha_i R_i$. And what is more, the processing efficiency for nutrients, k_i, and the mortality coefficients for phytoplankton, m_i, are the same in each block ($k_i = k$, $m_i = m$). The magnitude of coefficient α_i depends upon the illumination at the ith level, and since illumination declines with depth (i.e. with the block number), α_i may be represented in the form

$$\alpha_i = \alpha_S \exp\{-\beta_i\}, \qquad i = 1, \ldots, n \tag{8.2}$$

(α_S is the value of this coefficient on the surface).

Systems (8.1) and (8.1′) may have the following steady states:

$$\text{(a)}\quad R_i^* = \frac{m}{k\alpha_i}, \qquad N_i^* = q\left(\frac{1}{\alpha_{i+1}} - \frac{1}{\alpha_i}\right), \tag{8.3}$$

or

$$R_{i+1}^* = R_i^*, \qquad N_i^* = 0, \tag{8.3′}$$

$$\text{(b)}\quad R_i^* = \frac{m}{k\alpha_i}, \qquad N_i^* = D\left(\frac{1}{\alpha_{i+1}} - \frac{2}{\alpha_i} + \frac{1}{\alpha_{i-1}}\right), \tag{8.4}$$

or

$$R_i^* = (R_{i+1}^* + R_{i-1}^*)/2, \qquad N_i^* = 0. \tag{8.4′}$$

Here

$$R_{n+1}^* = R_b, \qquad R_0^* = 0, \qquad \alpha_{n+1} = \frac{m}{kR_b}, \qquad \frac{1}{\alpha_0} = 0.$$

Since $\alpha_{i-1} > \alpha_i$, at the points of non-trivial equilibrium (8.3) and (8.4) $R_{i-1}^* < R_i^*$ and $N_{i-1}^* < N_i^*$, i.e. both the equilibrium concentration of nutrients and the phytoplankton biomass are to increase with depth. How can we account for the really observed phytoplankton distribution? To tackle this problem we need to study the stability of steady states. We shall restrict ourselves to model (a) since the other model gives nothing new in principle.

The $2n \times 2n$ matrix A of the linearized system (8.1) has the following structure

$$A = \operatorname{diag}\{A_1, \ldots, A_n\} + Q, \tag{8.5}$$

where

$$A_i = \begin{Vmatrix} -q - \alpha_i N_i^* & -\alpha_i R_i^* \\ k\alpha_i N_i^* & k\alpha_i R_i^* - m \end{Vmatrix}, \tag{8.6}$$

and Q is a matrix with all the non-zero entries placed above the diagonal blocks A_i. Therefore, if $\mu_{1,2}^{(i)}$ are the eigenvalues of matrix A_i, then the eigenvalues of matrix A are equal to

$$\lambda_{2i-1} = \mu_1^{(i)}, \qquad \lambda_{2i} = \mu_2^{(i)}, \qquad i = 1, \ldots, n. \tag{8.7}$$

Let now the equilibrium $\mathbf{N}^*$ be such that the population in the ith block is $N_i^* > 0$. Then it follows from (8.3) and (8.6) that

$$\mu_{1,2}^{(i)} = -\frac{\alpha_i q}{2\alpha_{i+1}} \pm \sqrt{\left(\frac{\alpha_i q}{2\alpha_{i+1}}\right)^2 - mq\left(\frac{\alpha_i}{\alpha_{i+1}} - 1\right)}, \tag{8.8}$$

i.e. in this case if $N_i^* > 0$ then always $\mathrm{Re}\mu_{1,2}^{(i)} < 0$.

But if the equilibrium is trivial, that is $N_i^* > 0$, then

$$\mu_1^{(i)} = -q, \qquad \mu_2^{(i)} = k\alpha_i R_{i+1}^* - m, \tag{8.9}$$

and hence $\mathrm{Re}\,\mu_2^{(i)} < 0$ only when $m > k\alpha_i R_{i+1}^*$.

Let us show that if there exists a non-trivial equilibrium in the $(i+1)$th block, then the trivial equilibrium in the ith block will be unstable. In fact, since the equilibrium in the $(i+1)$th block is non-trivial, $R_{i+1}^* = m/(k\alpha_{i+1})$. But then for the trivial equilibrium it follows from (8.9) that

$$\mu_2^{(i)} = k\alpha_i R_{i+1}^* - m = m\left(\frac{\alpha_i}{\alpha_{i+1}} - 1\right).$$

Stability is only possible here when $\mu_2^{(i)} < 0$, i.e. for $\alpha_i < \alpha_{i+1}$, this contradicting the basic assumption about the decline of α_i with i. The contradiction proves our statement.

It follows immediately that the succession of blocks with stable trivial equilibrium may only be initiated from the last block. For the latter $\mu_2^{(n)} = k\alpha_n R_b - m$ and $\mu_{(2)}^{(n)} < 0$ only if $k\alpha_n R_b < m$. In the $(n-1)$th block the trivial equilibrium is to be stable (on the condition that the state with $N_n^* = 0$ is stable), when $k\alpha_{n-1}R_b < m$ and so on, until for some $(n-r)$th block it will be that $k\alpha_{n-r}R_b > m$. The last condition implies (besides instability of the trivial equilibrium in this block), that a non-trivial equilibrium with

$$N_{n-r}^* = q\left(\frac{R_b k}{m} - \frac{1}{\alpha_{n-r}}\right) > 0,$$

is possible in this block and it will be stable, just as in all the other blocks with smaller numbers. Obviously, the condition

$$k\alpha_{n-r}R_b = m$$

specifies the threshold depth level

$$i_{cr} = -\frac{1}{\beta}\ln m/\alpha_S k R_b, \tag{8.10}$$

below which the only stable equilibrium state for phytoplankton is the zero-biomass state. Figure 48 displays one of the possible stationary vertical distributions for phytoplankton, derived from the model (a). Clearly, the really observed distribution is continuous. The discontinuity of the distribution in Fig. 48 may be ascribed to the fact that in constructing the model we neglected the effects of

intermixing, always present in an ecosystem. The account of this factor automatically "erodes" the jump in the model distribution and brings about the continuous distribution better resembling the one observed in nature. For comparison the same figure depicts the really observed vertical distribution of phytoplankton in the ocean.

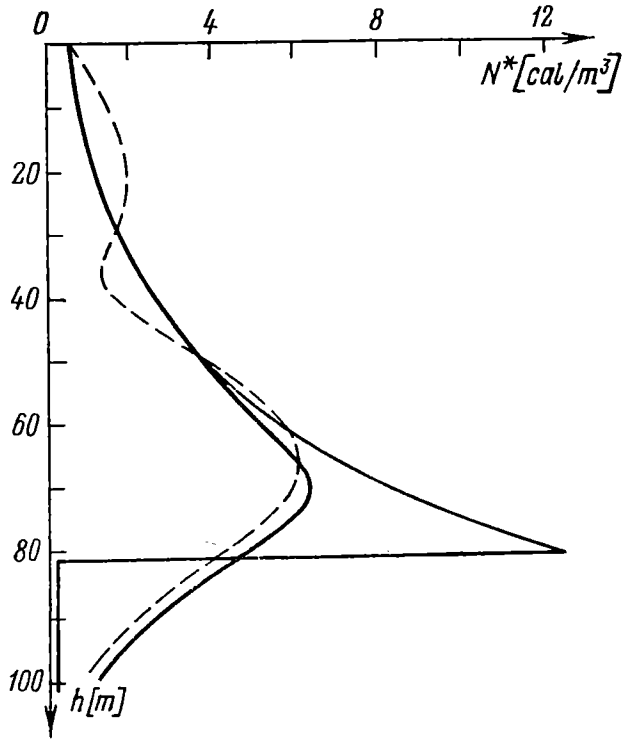

Fig. 48. Stationary vertical distribution of phytoplankton: —the distribution derived in model (8.1); $q = 1$, $R_b = 600$ cal/m³, $k = 0.4$, $m = 0.8$ 1/day, $\alpha_s = 0.086$ m³/cal·day, $\beta = 0.04$ 1/m; —the distribution derived from the theoretical one with account for the intermixing factor (the specific scale of vertical intermixing is 10 m); - - - vertical distribution of phytoplankton observed in experiments in Western Pacific. [From: *Operation of pelagic communities in trophic regions of the ocean.* Nauka, Moscow, 1961 (in Russian)].

The analyzed model gives a graphic illustration of the mechanism by which homogeneous in space stationary distributions for populations (biomasses) develop through a loss of stability in local nontrivial equilibria. The loss of stability, in turn, is due to dissimilar values of the system parameters at different points in space.

8.3. Can migration stabilize ecosystem?

In the preceding section we had an example of how environmental parameters being different at different spatial points results in a loss of stability in equilibrium states. The question arises: "What is

the influence of a spatially distributed pattern on stability, when the values of environmental parameters are the same?" We shall try to answer this question, considering the dynamics of several identical communities, linked together by migration flows.

Suppose, in the space there exist a number n of identical, relatively isolated habitats, each occupied by a community with the same collection of p species interacting with one another in the same way for all the habitats. Suppose also that individuals of species belonging to separate communities, according the radii of their individual activity, can pass from some habitats to other ones, i.e. there is a migration of species between communities. It is only natural to think that the intensity of migration is not independent of the populations of the migrating species in habitats which are sources and sinks in the migration process.

Clearly then the aggregate of n communities makes up a whole *system*—let us call it *united*—consisting of n *subsystems*. Within a subsystem species are connected by biological interactions, and migration flows run between subsystems. May we expect the united system to be stable, if all the isolated subsystems feature stability? Can the migration links stabilize an unstable behavior of isolated subsystems? Ecologists are inclined to give positive answers to these questions; and what may be derived from the study of mathematical models is to become clear from the following.

Let the dynamics of an isolated community be modeled by some system of equations

$$\frac{dN_i}{dt} = f_i(N_1, \ldots, N_p), \qquad i = 1, \ldots, p, \tag{8.11}$$

where the right-hand sides are restricted by the only qualitative requirements that the equilibrium $\mathbf{N}^* > \mathbf{0}$ exist and that linearization be possible at the point $\mathbf{N}^*$. When combining n such subsystems, the number of the appropriate subsystem will be labeled by the upper index for the variable N_i. Then

$$\frac{dN_i^k}{dt} = f_i(N_1^k, \ldots, N_p^k) + M_{ik}(N_i^1, \ldots, N_i^n), \tag{8.12}$$

$$k = 1, \ldots, n; \qquad i = 1, \ldots, p,$$

where the functions f_i specify the structure of biological interactions within the kth subsystem (arbitrary enough, but identical for all the subsystems), and the functions M_{ik} characterize the effect of migration flows from all the other subsystems into the kth one. These functions in their simplest, linear, form are associated with migration flows with intensities constant for the ith species and for a fixed *route* of migration (i.e. the direction $s \to k$). Obviously, the linear relationship is by no means the only type of relationship between migra-

tion and the populations of migrating species, however, because all the further results are derived by the linearization method, we may well confine ourselves to the linear approximation.

If we suppose that the scheme of the migration process (the routes of migrants between subsystems) is only determined by the geometry of relative positions of habitats in space (or, in other words, by geographical peculiarities), then clearly this scheme is to be the same for all the migrating species. In this case it may be represented by the single matrix of migration structure $M_n = \|m_{ks}\|$ $(k, s = 1, \ldots, n)$, where the entry $m_{ks} \geqslant 0$ $(k \neq s)$ specifies the migration intensity on the route $s \to k$.

The system being closed with respect to migration implies that

$$m_{kk} = -\sum_{\substack{s=1 \\ s \neq k}}^{n} m_{sk}, \qquad k = 1, \ldots, n. \tag{8.13}$$

Denoting by $m_i \geqslant 0$ the fraction of migration intensity that is only due to biological features of the ith species $(i = 1, \ldots, p)$ and is independent of the migration route, we get the system of equations for the united community in the form

$$\frac{dN_i^k}{dt} = f_i(N_1^k, \ldots, N_p^k) + m_i \sum_{s=1}^{n} m_{ks} N_i^s, \tag{8.14}$$

$i = 1, 2, \ldots, p$ — species number,

$k = 1, 2, \ldots, n$ — subsystem number.

The equality $m_i = 0$ indicates that the ith species (in all the subsystems) takes no part in migration.

If the migration intensity is entirely determined by biological features of species and is independent of the direction (the medium is isotropic with respect to migration), then all the non-zero non-diagonal elements of the matrix M_n are identical and just indicate that there is a migration between the two appropriate habitats (with the same intensity in both directions). In this case all these elements may be taken to be 1; matrix M_n is symmetric, and by (8.13) all the row sums in it are zero:

$$m_{kk} + \sum_{s \neq k}^{n} m_{ks} = 0. \tag{8.15}$$

It is readily seen that then the steady-state equations for the system (8.14),

$$f_i(N_1^k, \ldots, N_p^k) + m_i \sum_{s=1}^{n} m_{ks} N_i^s = 0 \tag{8.16}$$

$k = 1, \ldots, n; \qquad i = 1, \ldots, p,$

allow a solution in the form of an np-vector

$$\mathcal{N}^* = [\mathbf{N}^*, \ldots, \mathbf{N}^*],$$

which keeps all the previous equilibrium population values for isolated subsystems*. Linearization of (8.14) at a given point gives the matrix $\mathcal{A}$ with the block-diagonal structure

$$\mathcal{A} = \mathrm{I}_n \otimes \mathrm{A} + M_n \otimes D, \tag{8.17}$$

where

$$A = \left\| \frac{\partial f_i}{\partial N_j} \Big|_{N^*} \right\|$$

is the $p \times p$ matrix of the linearized isolated system, I_n is the $n \times n$ identity matrix, $D = \mathrm{diag}\ \{m_1, \ldots, m_p\}$ is the diagonal matrix of migration intensities, depending only on the biological peculiarities in each species, and the symbol $\otimes$ stands for the Kronecker matrix-product. We can judge about stability of the equilibrium $\mathcal{N}^*$ by the following lemma:

Lemma 1. Let matrix $M_n = \| m_{ks} \|$ have a zero eigenvalue and let $\mathbf{a} = [a_1, \ldots, a_n]$ be the eigenvector, belonging to the zero value. Then if $\mathbf{x} \in R^p$ is the column-eigenvector of matrix A with the eigenvalue λ, then the column-eigenvector $\mathcal{X} = [a_1\mathbf{x}, \ldots, a_n\mathbf{x}]^T$ of matrix $\mathcal{A}$ from (8.17) also belongs to this value.

Proof. Using the methods of operating with block matrices of consistent structure**, we get

$$\mathcal{A}(\mathcal{X}) = \mathcal{A}(\mathbf{a} \otimes \mathbf{x}) = \begin{bmatrix} (A + m_{11}D)\, a_1\mathbf{x} + m_{12}Da_2\mathbf{x} + \ldots + m_{1n}Da_n\mathbf{x} \\ m_{21}Da_1\mathbf{x} + (A + m_{22}D)\, a_2\mathbf{x} + \ldots + m_{2n}Da_n\mathbf{x} \\ \cdots\cdots\cdots\cdots\cdots\cdots \\ m_{n1}Da_1\mathbf{x} + m_{n2}Da_2\mathbf{x} + \ldots + (A + m_{nn}D)\, a_n\mathbf{x} \end{bmatrix}$$

$$= \begin{bmatrix} a_1A\mathbf{x} + (m_{11}a_1 + m_{12}a_2 + \ldots + m_{1n}a_n)\, D\mathbf{x} \\ a_2A\mathbf{x} + (m_{21}a_1 + m_{22}a_2 + \ldots + m_{2n}a_n)\, D\mathbf{x} \\ \cdots\cdots\cdots\cdots\cdots\cdots \\ a_nA\mathbf{x} + (m_{n1}a_1 + m_{n2}a_2 + \ldots + m_{nn}a_n)\, D\mathbf{x} \end{bmatrix} = \begin{bmatrix} a_1\lambda\mathbf{x} \\ a_2\lambda\mathbf{x} \\ \cdots \\ a_n\lambda\mathbf{x} \end{bmatrix} = \lambda\mathcal{X},$$

Q.E.D.

According to (8.15) matrix M_n of a closed migration pattern has an eigenvector $a = [1, 1, \ldots, 1]$ with $\lambda = 0$ in an isotropic environ-

* Clearly, in the general case there may be other, additional solutions to (8.6), with all the components being positive. It may be proved, for instance, that there are no such solutions, when two conservative Volterra subsystems of order two are united.

** See Gantmacher F. R., *The Theory of Matrices*, Vol. 1, Chelsea, New York, 1960.

ment, i.e. satisfies the conditions of Lemma 1. Thus the spectrum of matrix $\mathcal{A}$ for the united system necessarily contains the set of all eigenvalues λ_i, which determine the stability of equilibrium $\mathbf{N}^*$ in the isolated subsystem.This means that if $\mathbf{N}^*$ was unstable in the subsystem (i.e. there existed eigenvalues of A with $\operatorname{Re}\lambda(A) > 0$), then the instability is also preserved in system (8.14); if matrix A was stable (all $\operatorname{Re}\lambda(A) < 0$), then for the equilibrium $\mathcal{N}^*$ to be

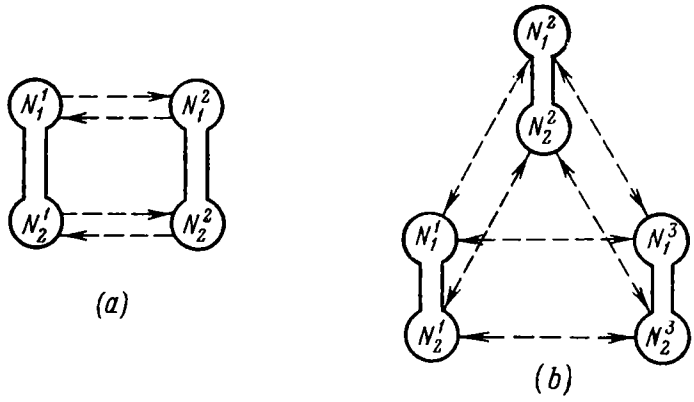

Fig. 49. Examples of migration patterns. Broken arrows show flows of migrants; interaction within habitats is not specified.

stable in the united system the real parts of all the remaining eigenvalues for matrix $\mathcal{A}$ are required to be negative, thus somehow reducing (or making empty) the stability domain in the space of model parameters.

If A has a real spectrum, whereas among the additional values arising from the spectrum of $\mathcal{A}$ there are complex ones, then the steady behavior of trajectories in the neighborhood of the equilibrium for the isolated subsystem is replaced by oscillations. The reverse interchange evidently cannot take place, since the spectrum of A is preserved.

Example 1. Let $n = p = 2$ (see Fig. 49*a*). Then the united system is of the fourth order:

$$dN_1^1/dt = f_1(N_1^1, N_2^1) + m_1(-N_1^1 + N_1^2),$$

$$dN_2^1/dt = f_2(N_1^1, N_2^1) + m_2(-N_2^1 + N_2^2),$$

$$dN_1^2/dt = f_1(N_1^2, N_2^2) + m_1(N_1^1 - N_1^2),$$

$$dN_2^2/dt = f_2(N_1^2, N_2^2) + m_2(N_2^1 - N_2^2);$$

$$M_2 = \begin{Vmatrix} -1 & 1 \\ 1 & -1 \end{Vmatrix}, \qquad D = \begin{Vmatrix} m_1 & 0 \\ 0 & m_2 \end{Vmatrix}.$$

Denoting the elements of matrix $A = \| \partial f_i/\partial N_j \|_{N^*}$ by

$$A = \begin{Vmatrix} a & b \\ c & d \end{Vmatrix},$$

we get the matrix of the united system

$$\mathcal{A} = \left\| \begin{array}{cc|cc} a-m_1 & c & m_1 & 0 \\ b & d-m_2 & 0 & m_2 \\ \hline m_1 & 0 & a-m_1 & c \\ 0 & m_2 & b & d-m_2 \end{array} \right\|$$

with the characteristic polynomial

$$[(\lambda-a)(\lambda-d)-bc]\,\{[\lambda-(a-2m_1)]\,[\lambda-(d-2m_2)]-bc\}=0,$$

which along with the roots of the isolated subsystem

$$\lambda_{1,2}=\frac{1}{2}(a+d\pm\sqrt{(a-d)^2+4bc}),$$

has a pair of new roots

$$\lambda_{3,4}=\frac{1}{2}(\tilde{a}+\tilde{d}\pm\sqrt{(\tilde{a}-\tilde{d})^2+4bc}), \qquad \tilde{a}=a-2m_1, \qquad \tilde{d}=d-2m_2.$$

The stability criterion based on the linear approximation gives the conditions

$$a+d<0, \qquad ad-bc>0, \tag{8.18}$$

$$\tilde{a}+\tilde{d}<0, \qquad \tilde{a}\tilde{d}-bc>0, \tag{8.18'}$$

and if they are satisfied, then all the Re λ_i are negative.

It is clear that if the inequalities (8.18) hold—the stability conditions for an isolated subsystem—then for sufficiently small m_1 and m_2 (8.18′) is also satisfied, i.e. the united system is stable as well. If the trajectories of the isolated subsystem are monotonically stable in the neighborhood of $\mathbf{N}^*$, which is the case when

$$(a-d)^2+4bc\geqslant 0, \qquad ad-bc>0, \tag{8.19}$$

then the stable trajectories remain monotonic in the united system provided that

$$(\tilde{a}-\tilde{d})^2+4bc\geqslant 0, \qquad \tilde{a}\tilde{d}-bc>0. \tag{8.19'}$$

When condition (8.19) holds, obviously (8.19′) is also satisfied for sufficiently small m_1 and m_2. But if m_1 and m_2 are such that the first condition in (8.19′) fails, i.e. there appear the complex conjugate roots $\lambda_{3,4}$ and the condition $\tilde{a}+\tilde{d}<0$ is satisfied, then the steady behavior of stable trajectories in the isolated subsystem is replaced by an oscillatory-stable behavior of trajectories in the united sys-

tem. The inverse replacement cannot take place due to the presence of the pair of roots $\lambda_{1,2}$ from the isolated subsystem in the spectrum of $\mathcal{A}$, i.e. if the subsystem demonstrated oscillations when approaching the equilibrium $\mathbf{N}^*$, then the oscillations are preserved after the integration into a system.

In a like manner one may consider the conditions under which monotonic instability features oscillations after integration.

But if under the conditions of (8.18) the second inequality in (8.18′) is changed for the opposite (obviously, the first one remains satisfied), then the equilibrium of the united system turns to be unstable, that is, migration destabilizes the system.

Example 2. Another example of a migration pattern is given in Fig. 49*b*, where $n = 3$. Migration here occurs with the same intensity between any two of the n habitats, this may be explained by them being mutually equidistant in the plane. In a three-dimensional space similar geometric considerations result in four habitats placed at the vertices of a regular tetrahedron. For $n \Rightarrow 4$ similar geometric constructions become impossible in a 3-dimensional space.

The matrix of the migration pattern (in the isotropic case) has the form

$$M_n = \begin{Vmatrix} -(n-1) & 1 & 1 \ldots & 1 \\ 1 & -(n-1) & 1 \ldots & 1 \\ \cdots & \cdots & \cdots & \cdots \\ 1 & 1 & 1 \ldots & -(n-1) \end{Vmatrix} \tag{8.20}$$

and satisfies the conditions of Lemma 1.

Generally, one may think of even more complex schemes of linking the subsystems than those illustrated in Fig. 49*a*, *b*. Lemma 1 enables us to state that the original eigenvalues are preserved in the spectrum of the united system for any migration pattern M_n with zero row-sums. Since the last condition is also a criterion that the previous equilibrium values are retained in the steady-state solution to the united system (8.16), this results in the following conclusion: if the integration according to some migration scheme preserves the equilibrium values of the isolated subsystems, then the spectrum of the united system keeps the previous eigenvalues and the above statements as to the behavior of trajectories in the neighborhood of equilibrium are valid.

In the special case where all the "biological" migration intensities are the same, i.e.

$$m_i = m, \qquad i = 1, \ldots, p,$$

the techniques of Kronecker matrix-products enables us to derive the explicit form for all the eigenvalues of the united system. In fact, in

this case

$$\mathcal{A} = I_n \otimes A + mM_n \otimes I_p, \tag{8.21}$$

and for known $\lambda(A)$ and $\lambda(M_n)$ we can find $\lambda(A)$ using Lemma 2.

Lemma 2. Let X and Y be $p \times p$ and $n \times n$ matrices, respectively, with eigenvalues λ_i $(i = 1, \ldots, p)$ and μ_j $(j = 1, \ldots, n)$. Then the eigenvalues of matrix $I_n \otimes X + Y \otimes I_p$ are all possible values of sums $\lambda_i + \mu_j$.

Proof. Let $\mathbf{x}^i$ and $\mathbf{y}^j$ be the eigenvectors of matrices X and Y, respectively, belonging to the eigenvalues λ_i and μ_j. Consider the matrix $(I_n + Y) \otimes (I_p + X)$. The eigenvalues of the multipliers are $1 + \mu_j$ and $1 + \lambda_i$, respectively. The eigenvalues of the Kronecker product are all possible pairwise products of eigenvalues of multipliers, which are associated with the eigenvectors of the form

$$\mathfrak{Z}^{ji} = [y_1^j \mathbf{x}_2^j,\ y^j \mathbf{x}^i,\ \ldots,\ y_n^j \mathbf{x}^i].$$

Further, because

$$(I_n + Y) \otimes (I_p + X) = I_n \otimes I_p + I_n \otimes X + Y \otimes I_p + Y \otimes X$$
$$= I_{np} + (I_n \otimes X + Y \otimes I_p) + Y \otimes X,$$

we have

$$(1 + \mu_j)(1 + \lambda_j)\mathfrak{Z}^{ji} = \mathfrak{Z}^{ji} + (I_n \otimes X + Y \otimes I_p)\mathfrak{Z}^{ji} + \mu_j \lambda_i \mathfrak{Z}^{ji}.$$

Multiplying out in the left-hand side of this equation, we get

$$(\lambda_i + \mu_j)\mathfrak{Z}^{ji} = (I_n \otimes X + Y \otimes I_p)\mathfrak{Z}^{ji},$$

whence follows the statement of the lemma.

If applied to matrix $\mathcal{A}$ from (8.21) Lemma 2 states that the eigenvalues of $\mathcal{A}$ are all possible pairwise sums

$$\lambda(\mathcal{A}) = \lambda_i + m\mu_j,$$

where λ_i and μ_j are the eigenvalues of A and M_n, respectively.

Example 3. For the migration pattern, resulting from the "annular" arrangement of habitats, similar to the annular arrangement of ecological niches for competing species (cf. Fig. 44 in Chapter 6), the matrix of the migration pattern in an isotropic medium is the circulant

$$M_n = \begin{Vmatrix} -2 & 1 & 0 & \ldots & 0 & 1 \\ 1 & -2 & 1 & \ldots & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 1 & 0 & 0 & \ldots & 1 & -2 \end{Vmatrix},$$

with the eigenvalues

$$\mu_j = -2 + \cos j\frac{2\pi}{n} + \cos j\frac{2\pi(n-1)}{n}$$
$$= -2\left(1 - \cos j\frac{2\pi}{n}\right), \quad j = 0, 1, \ldots, n-1.$$

In the special case of equal $m_i = m$ the eigenvalues for $\mathcal{A}$ are

$$\lambda(\mathcal{A}) = \lambda_i + m\mu_j.$$

The presence of a $\mu_0 = 0$ bears out the conclusion about the preservation of all the original eigenvalues λ_i, and as long as all the other μ_i are real and $\mu_j < 0$, we can say that integration by no means affects stability as compared with the isolated case and the qualitative picture of trajectories behavior in the neighborhood of equilibrium remains unchanged.

Summarizing our analysis of migration patterns in isotropic medium, we see (Lemma 1) that for any structure of biological interactions is an isolated subsystem integration by means of migration fails to improve the system properties from the viewpoint of stability, it rather may only replace the steady behavior of trajectories in the neighborhood of equilibrium (stable or unstable) by oscillations, but not vice versa. In some cases such an integration may even destabilize stable subsystems (Cf. Example 1).

As it was shown, the basis for these mathematical results is provided by singularity of the matrix of migration pattern M_n in an isotropic medium. At the same time it is difficult to imagine that any real environment, with some prevailing directions of migration practically always present, could ensure strict isotropy on all routes. The stabilizing effects of migration, observed in experiments, seem to be explained by distinctions in migration intensities in different directions, and within the framework of mathematical models such effects are to be sought in schemes with intensities essentially depending upon the direction, i.e. for environments, *anisotropic* with respect to migration. In the two following sections schemes of this kind are considered.

8.4. Migration in anisotropic environment

We turn now to the case, where migration intensity depends not only upon the biological peculiarities of migrating species, but also upon the route, i.e. the direction of migration; in other words, we suppose that the environment is *anisotropic* with respect to migration. The influence of environmental anisotropy will be studied referring to a system with $n = 2$ habitats, within which (in an identical way, as before) interact $p = 2$ biological species with populations $x(t)$ and $y(t)$:

$$\begin{aligned} \frac{dx}{dt} &= f_x(x, y), \\ \frac{dy}{dt} &= f_y(x, y) \end{aligned} \tag{8.22}$$

Simplifying the notations of the preceding section, assume that

$$(m_{12})_x = r + \rho, \qquad (m_{21})_x = r - \rho,$$
$$(m_{12})_y = s + \sigma, \qquad (m_{21})_y = s - \sigma \tag{8.23}$$

and notice that the variables ρ and σ specify the distinctions in intensities of migration in opposite directions; the case of $\rho = \sigma = 0$ corresponds to the scheme of the preceding section. Let for definiteness $(m_{12})_x > (m_{21})_x$ and $(m_{12})_y > (m_{21})_y$. Then it is clear that, using the adopted notations

$$0 < \rho < r, \qquad 0 < \sigma < s.$$

Dynamics of the integrated community is modeled by a fourth-order system:

$$\begin{aligned}
\dot{x}^1 &= f_x(x^1, y^1) - (r - \rho)x^1 + (r + \rho)x^2,\\
\dot{y}^1 &= f_y(x^1, y^1) - (s - \sigma)y^1 + (s + \sigma)y^2,\\
\dot{x}^2 &= f_x(x^2, y^2) + (r - \rho)x^1 - (r + \rho)x^2,\\
\dot{y}^2 &= f_y(x^2, y^2) + (s - \sigma)y^1 - (s + \sigma)y^2.
\end{aligned} \tag{8.24}$$

The fact that migration actually takes place for at least one of the species and with intensity that varies with direction is expressed by the conditions

$$r + s > 0, \qquad \rho^2 + \sigma^2 \neq 0.$$

If there is a non-trivial equilibrium $\mathbf{z}^* = [\overset{*}{x}{}^1, \overset{*}{y}{}^1, \overset{*}{x}{}^2, \overset{*}{y}{}^2]$ for system (8.24), then linearization around this equilibrium gives the matrix

$$\mathcal{A}(\mathbf{z}^*) = \begin{Vmatrix} A(\overset{*}{x}{}^1, \overset{*}{y}{}^1) - \operatorname{diag}\{r-\rho,\ s-\sigma\} & \operatorname{diag}\{r+\rho,\ s+\sigma\} \\ \operatorname{diag}\{r-\rho,\ s-\sigma\} & A(\overset{*}{x}{}^2, \overset{*}{y}{}^2) - \operatorname{diag}\{r+\rho,\ s+\sigma\} \end{Vmatrix}, \tag{8.25}$$

where $A(\overset{*}{x}{}^i, \overset{*}{y}{}^i)$ are matrices of subsystems, linearized at the points $[\overset{*}{x}{}^i, \overset{*}{y}{}^i]$. By the spectrum of matrix $\mathcal{A}(\mathbf{z}^*)$, as usually we shall judge about stability for the equilibrium $\mathbf{z}^*$, and comparing this spectrum with the eigenvalues of matrix $A(x^*, y^*)$ we can draw conclusions about the effect of migration on the system stability.

The original equilibrium values for populations x^* and y^*—such that $f_x(x^*, y^*) = f_y(x^*, y^*) = 0$—are not preserved in this system. It is natural to suppose that as a result of non-symmetric migration the equilibrium populations are so redistributed, that the new

equilibria are

$$\overset{*}{x}{}^1 = x^* + \Delta x, \qquad \overset{*}{y}{}^1 = y^* + \Delta y,$$
$$\overset{*}{x}{}^2 = x^* - \Delta x, \qquad \overset{*}{y}{}^2 = y^* - \Delta y. \tag{8.26}$$

It is easily shown that for such a stationary solution to exist in system (8.24) it is necessary for the functions $f_x(x, y)$ and $f_y(x, y)$ to feature *skew-symmetry* at the point $[x^*, y^*]$ with respect to the increments Δx and Δy:

$$f_{x(y)}(x^* + \Delta x,\ y^* + \Delta y) = -f_{x(y)}(x^* - \Delta x,\ y^* - \Delta y).$$

In fact, if we insert (8.26) into the steady-state equations for system (8.24), we get the equations

$$\begin{aligned} 2\rho x^* - 2r\Delta x + f_x(x^* + \Delta x,\ y^* + \Delta y) &= 0, \\ -2\rho x^* + 2r\Delta x + f_x(x^* - \Delta x,\ y^* - \Delta y) &= 0, \\ 2\sigma y^* - 2s\Delta y + f_y(x^* + \Delta x,\ y^* + \Delta y) &= 0, \\ -2\sigma y^* + 2s\Delta y + f_y(x^* - \Delta x,\ y^* - \Delta y) &= 0, \end{aligned} \tag{8.27}$$

which, when added pairwise, give the needed relationships. Let us see if these conditions are satisfied, say, for the Volterra description of the predator-prey type interactions with no self-regulation, that is, when

$$f_x = \alpha x - \beta xy \qquad (\alpha,\ \beta,\ \gamma,\ \delta > 0), \qquad x^* = \gamma/\sigma;$$
$$f_y = -\gamma y + \delta xy \qquad\qquad y^* = \alpha/\beta.$$

The predator-prey models represent, perhaps, the most interesting object for the study of migration effects: in this case usually the equilibrium is neutrally stable and we can expect that migration effects will alter the behavior in either direction.

The conditions of skew-symmetry for the above written functions require that

$$2\beta\Delta x\Delta y = 0, \qquad 2\delta\Delta x\Delta y = 0,$$

this being possible only if $\Delta x = 0$ or $\Delta y = 0$ (the case of $\Delta x = \Delta y = 0$ belongs to isotropic medium). For $\Delta x = 0$ the system (8.27), allowing for the condition that $y^* \pm \Delta y > 0$, gives the solution of the form

$$\Delta x = 0, \qquad \Delta y = 2\frac{\rho}{\beta}, \qquad \alpha > 2\rho \text{ for } s = \sigma = 0$$
$$\text{or for } \alpha\sigma/s = 2\rho, \qquad s,\ \sigma,\ \rho > 0. \tag{8.28a}$$

For $\Delta y = 0$, allowing for the condition that $x^* \pm \Delta x > 0$, likewise we get

$$\Delta y = 0, \qquad \Delta x = -2\sigma/\delta, \qquad \gamma > 2\,|\,\sigma\,| \qquad \text{for } r = \rho = 0$$
$$\text{or for } \gamma\rho/r = -2\sigma, \qquad r,\ \rho > 0, \qquad \sigma < 0. \tag{8.28b}$$

So the case of (8.28a) is possible either when there is no migration of predators at all, or when the parameters of this migration satisfy a specific relationship, and the migration among the preys occurs in the same direction as with predators (σ and ρ have the same sing). In this case the original equilibrium values for the prey populations x^* are preserved, and the predator population is increased by $\Delta y > 0$ in the subsystem into which the migration is preferable (the first one in this case). It may be said that the relationship (8.28a) between system parameters ensures that the increased predator population will uptake the excess in preys resulting in the first subsystem from favourable migration. The relationship

$$\alpha\sigma/s = 2\rho$$

suggests that the point that characterizes the system in the space of all model parameters is projected into the 3-dimensional space of parameters $\{\alpha, \sigma/s, \rho\}$ onto the part of a second-order surface (hyperbolic paraboloid) bounded by the plane $\sigma/s = 1$ in the positive orthant (the condition $\alpha > 2\rho$ is automatically met).

The case of (8.28b) is possible either when there is no migration of prey at all, or when the parameters of migration satisfy a special relationship, and the migration of predators for the most part is in the opposite direction (σ and ρ are opposite in sign). The preservation of equilibrium values y^* and the redistribution in x^* may be interpreted so, that the excess in predators resulting in the second subsystem from favourable migration vanishes because of the reduced (due to preferred migration in the opposite direction) population of the prey in this subsystem. As in the case of (8.28a) the point, which specifies the system in the space of parameters, is projected onto a similar surface, but now in the space $\{\gamma, \rho/r, -\sigma\}$.

Examine the equilibrium stability in the case where two predator-prey pairs are linked by migration in the level of preys with the preferred direction $2 \to 1$. System (8.24) may then be written in the form

$$\begin{aligned}
\dot{x}^1 &= \alpha x^1 - \beta x^1 y^1 - (r - \rho)x^1 + (r + \rho)x^2, \\
\dot{y}^1 &= -\gamma y^1 + \delta x^1 y^1, \\
\dot{x}^2 &= \alpha x^2 - \beta x^2 y^2 + (r - \rho)x^1 - (r + \rho)x^2, \\
\dot{y}^2 &= -\gamma y^2 + \delta x^2 y^2
\end{aligned} \tag{8.29}$$

and it features a positive equilibrium of the type (8.28a), when $\alpha > 2\rho$ that is

$$\overset{*}{x}{}^{1,2} = x^* = \gamma/\delta, \qquad \overset{*}{y}{}^{1,2} = y^* \pm \Delta y = (\alpha \pm 2\rho)/\beta. \tag{8.30}$$

Matrix (8.25) takes the form

$$\mathcal{A} = \left\| \begin{array}{cc|cc} -r-\rho & -\beta\gamma/\delta & r+\rho & 0 \\ \delta(\alpha+2\rho)/\beta & 0 & 0 & 0 \\ \hline r-\rho & 0 & -r+\rho & -\beta\gamma/\delta \\ 0 & 0 & \delta(\alpha-2\rho)/\beta & 0 \end{array} \right\| \tag{8.31}$$

and has the characteristic polynomial

$$\lambda^4 + 2r\lambda^3 + 2\alpha\gamma\lambda^2 + 2\gamma(\alpha r - 2\rho^2)\lambda + \gamma^2(\alpha^2 - 4\rho^2) = 0. \tag{8.32}$$

In order to locate the eigenvalues λ in the complex plane utilize the well-known criterion of Routh-Hurwitz. The Hurwitz matrix for the polynomial (8.32) has the form

$$H = \left\| \begin{array}{cccc} 2r & 2\gamma(\alpha r - 2\rho^2) & 0 & 0 \\ 1 & 2\alpha\gamma & \gamma^2(\alpha^2 - 4\rho^2) & 0 \\ 0 & 2r & 2\gamma(\alpha r - 2\rho^2) & 0 \\ 0 & 1 & 2\alpha\gamma & \gamma^2(\alpha^2 - 4\rho^2) \end{array} \right\|,$$

whence the Hurwitz determinants will be

$$\begin{aligned} \Delta_1 &= H\begin{pmatrix} 1 \\ 1 \end{pmatrix} = 2r, \\ \Delta_2 &= H\begin{pmatrix} 1, & 2 \\ 1, & 2 \end{pmatrix} = 2\gamma(\alpha r + 2\rho^2), \\ \Delta_3 &= H\begin{pmatrix} 1, & 2, & 3 \\ 1, & 2, & 3 \end{pmatrix} = 16\gamma^2\rho^2(r^2 - \rho^2), \\ \Delta_4 &= \det H = \gamma^2(\alpha^2 - 4\rho^2)\Delta_3. \end{aligned} \tag{8.33}$$

The Routh-Hurwitz theorem states that for real parts of all the roots of a real polynomial to be negative it is necessary and sufficient that the conditions

$$a_0\Delta_1 > 0, \qquad \Delta_2 > 0, \ldots, \begin{cases} a_0\Delta_n > 0 & \text{(for odd } n), \\ \Delta_n > 0 & \text{(for even } n) \end{cases} \tag{8.34}$$

be satisfied (a_0 is the leading coefficient of the polynomial).

Remember that all the symbols appearing in the formulas (8.33) stand for positive parameters, and that $r \geqslant \rho$ follows from the definition of r and ρ, and $\alpha > 2\rho$ from the existence condition for a positive stationary point (8.30). Thus, except for the case where $\rho = r$ all the conditions of (8.34) are met, i.e. for all the eigenvalues of matrix (8.31)

$$\operatorname{Re} \lambda_i(\mathcal{A}) < 0, \qquad i = 1, \ldots, 4.$$

The equilibrium (8.30) is thereby asymptotically stable. If we now recall that for isolated predator-prey pairs the equilibrium $[x^*, y^*]$ is neutrally stable (with the frequency of oscillations $\omega = \sqrt{\alpha\gamma}$), it becomes clear, that our system (8.29) is an example of a stabilizing effect of migration.

The case of $\rho = r > 0$ implies that migration (with the intensity $2r$) goes only in one direction—from the second subsystem to the first. The spectrum of $\mathcal{A}$ [the roots of (8.32)] includes a pair of purely imaginary numbers

$$\lambda_{1,2} = \pm i\sqrt{\gamma(\alpha - 2\rho)}$$

and a pair of negative numbers

$$\lambda_{3,4} = -r \pm \sqrt{r^2 + 2\gamma r - \alpha\gamma}.$$

This means that in the united system the equilibrium (8.30) keeps the neutrally stable behavior typical of the isolated subsystems, however, the frequency of oscillations around the equilibrium (in the linear approximation) is equal to $\sqrt{\gamma(\alpha - 2\rho)}$, i.e. it is reduced as against the isolated case. According to some ecological ideas, the lesser frequency of oscillations makes for greater stability of the ecosystem, so in this sense we again have an example of the stabilizing effect of migration.

In a like manner we can study the system accounting for migration, which only occurs on the level of predators with the preferred direction $2 \to 1$:

$$\begin{aligned}
\dot{x}^1 &= \alpha x^1 - \beta x^1 y^1, \\
\dot{y}^1 &= -\gamma y^1 + \delta x^1 y^1 - (s - \sigma)y^1 + (s + \sigma)y^2 \\
&\qquad (r = \rho = 0;\ s,\ \sigma > 0), \qquad (8.35) \\
\dot{x}^2 &= \alpha x^2 - \beta x^2 y^2 \\
\dot{y}^2 &= -\gamma y^2 + \delta x^2 y^2 + (s - \sigma)y^1 - (s + \sigma)y^2.
\end{aligned}$$

At the equilibrium of the type (8.28b), which exists for $\gamma > 2\sigma$ we have

$$\overset{*}{y}{}^{1,2} = y^* = \alpha/\beta, \qquad \overset{*}{x}{}^{1,2} = x^* \pm \Delta x = (\gamma \mp 2\sigma)/\delta, \qquad (8.36)$$

i.e. $\overset{*}{x}{}^1 < \overset{*}{x}{}^2$. Spectral analysis for the matrix of system (8.35), linearized at this equilibrium, indicates that, just as in the previous case, all $\operatorname{Re} \lambda_i(\mathcal{A}) < 0$ except for the case of $\sigma = s > 0$. Thus the equilibrium (8.36) is asymptotically stable, i.e. system (8.35) again shows the stabilizing effect of migration.

The equality $\sigma = s$ implies that migration with the intensity $2s$ occurs only from the second subsystem to the first; as a result a pair of purely imaginary numbers appears

$$\lambda_{1,2} = \pm i \sqrt{\alpha(\gamma + 2s)}$$

and also a pair of negative numbers

$$\lambda_{3,4} = -s \pm \sqrt{s^2 + 2\alpha s - \alpha\gamma},$$

i.e. unidirectional migration of predators increases the frequency of oscillations around equilibrium as compared with the isolated case, and in this sense reduces the system stability.

Consider now the instances where migration takes place on both levels, but its parameters are related by (8.28a) or (8.28b). Of course, as it was already noted by V. Volterra, it is hardly probable that parameters of a real system would be restricted by some relationships of the equality type, but for mathematical completeness we shall examine those improbable cases. When the preferred direction of migration is the same with the predators and the preys (from the second subsystem into the first), system (8.24) takes the form

$$\begin{aligned}
\dot{x}^1 &= \alpha x^1 - \beta x^1 y^1 - (r - \rho)\, x^1 + (r + \rho)\, x^2, \\
\dot{y}^1 &= -\gamma y^1 + \delta x^1 y^1 - (s - \sigma)\, y^1 + (s + \sigma)\, y^2, \\
\dot{x}^2 &= \alpha x^2 - \beta x^2 y^2 + (r - \rho)\, x^1 - (r + \rho)\, x^2, \\
\dot{y}^2 &= -\gamma y^2 + \delta x^2 y^2 + (s - \sigma)\, y^1 - (s + \sigma)\, y^2.
\end{aligned} \tag{8.37}$$

The search for stationary solutions in the form $\overset{*}{x}{}^1 = \overset{*}{x}{}^2$ or $\overset{*}{y}{}^1 = \overset{*}{y}{}^2$ shows that equilibria of the (8.28a) or (8.28b) types are the only stationary solutions, which have equal populations on the same levels of the subsystems. (Notice that the last condition may be checked in experiment.)

Linearization of (8.37) at the point (8.30) under the condition that $\alpha\sigma = 2\rho s$, gives the matrix

$$\mathcal{A} = \left\| \begin{array}{cc|cc}
-r-\rho & -\beta\gamma/\delta & r+\rho & 0 \\
\delta(\alpha+2\rho)/\beta & -s+\sigma & 0 & s+\sigma \\
\hline
r-\rho & 0 & -r+\rho & -\beta\gamma/\delta \\
0 & s-\sigma & \delta(\alpha-2\rho)/\beta & -s-\sigma
\end{array} \right\|, \tag{8.38}$$

with the characteristic polynomial

$$\begin{aligned}
&\lambda^4 + 2(r + s)\lambda^3 + 2(\alpha\gamma + 2rs)\lambda^2 + 2\gamma\,[\alpha\,(r + s) - \\
&\quad - 2\rho\,(\rho - \sigma)]\lambda + \gamma^2\,(\alpha^2 - 4\rho^2) + 4\alpha\gamma\,(rs - \rho\sigma).
\end{aligned} \tag{8.39}$$

The Hurwitz determinants for this polynomial are equal to

$$\Delta_1 = 2\,(r + s)$$

$$\Delta_2 = 2\,[(r + s)\,(\alpha\gamma + 4rs) + 2\gamma\rho\,(\rho - \sigma)];$$

$$\Delta_3 = 16\,\{(r + s)\,[\alpha\gamma\sigma\,(r\sigma + s\rho) + (r + s)\,\gamma^2\rho^2] - \gamma^2\rho^2\,(\rho - \sigma)^2\};$$

$$\Delta_4 = [\gamma^2\,(\alpha^2 - 4\rho^2) + 4\alpha\gamma\,(rs - \rho\sigma)]\,\Delta_3.$$

Clearly $\Delta_1 > 0$. Positiveness of Δ_2 is also obvious, when $\rho - \sigma \geqslant 0$, otherwise, since $\sigma \leqslant s$ and $2\rho s = \alpha\sigma$,

$$\frac{1}{2}\Delta_2 = (r + s)\,(\alpha\gamma + 4rs) + 2\gamma\rho\,(\rho - \sigma)$$

$$\geqslant (r + s)\,(\alpha\gamma + 4rs) - 2\gamma\rho s = (r + s)\,(\alpha\gamma + 4rs) - \alpha\gamma\sigma$$

$$= r\,(\alpha\gamma + 4rs) + 4rs^2 + \alpha\gamma\,(s - \sigma) > 0.$$

Positiveness of Δ_3 is equivalent to the condition

$$(\rho + \sigma)^2 < \frac{r + s}{\gamma^2\rho^2}\,[\alpha\gamma\sigma\,(r\sigma + s\rho) + (r + s)\,\gamma^2\rho^2]$$

$$= \frac{\alpha\sigma}{\gamma\rho^2}\,(r + s)\,(r\sigma + s\rho) + (r + s)^2,$$

which is automatically satisfied, since it follows from the restrictions $0 < \rho \leqslant r$ and $0 < \rho \leqslant s$ that $(\rho + \sigma)^2 \leqslant (r + s)^2$. Positiveness of Δ_4 is equivalent to the condition

$$\gamma^2\,(\alpha^2 - 4\rho^2) + 4\alpha\gamma\,(rs - \rho\sigma) > 0,$$

which holds by virtue of the above-mentioned restrictions and the condition that $\alpha - 2\rho > 0$.

Thus, all the Hurwitz determinants are positive, accordingly, by the Routh-Hurwitz criterion matrix (8.38)—along with the equilibrium (8.30) in the system (8.37)—are stable.

The equilibrium of the type (8.28b) is possible, when prevailing migration is on the levels of predators and preys have opposite direction. To keep all the parameters positive rewrite system (8.37) in the form (replacing everywhere σ by $-\sigma$)

$$\begin{aligned}
\dot{x}^1 &= \alpha x^1 - \beta x^1 y^1 - (r - \rho)\,x^1 + (r + \rho)\,x^2,\\
\dot{y}^1 &= -\gamma y^1 + \delta x^1 y^1 - (s + \sigma)\,y^1 + (s - \sigma)\,y^2,\\
\dot{x}^2 &= \alpha x^2 - \beta x^2 y^2 + (r - \rho)\,x^1 - (r + \rho)\,x^2,\\
\dot{y}^2 &= -\gamma y^2 + \delta x^2 y^2 + (s + \sigma)\,y^1 - (s - \sigma)\,y^2.
\end{aligned} \tag{8.40}$$

Arguing along the same lines we may prove that the spectrum of system (8.40), linearized at the point

$$\overset{*}{y}{}^{1;2} = y^* = \alpha/\beta, \qquad \overset{*}{x}{}^{1;2} = x^* \pm \Delta x = (\gamma \pm 2\sigma)/\delta$$

$$(\gamma - 2\sigma > 0, \qquad \gamma\rho = 2r\sigma, \qquad \rho,\ \sigma > 0),$$

has negative real parts only under additional restrictions on the set of admissible values for model parameters:

$$(r+s)^2(\alpha\sigma-\gamma\rho)+(r+s)\,2rs\,(\rho+\sigma)-\alpha\sigma(\rho+\sigma^2)>0. \quad (8.42)$$

When the left-hand side in the inequality (8.42) vanishes, the spectrum contains a pair of purely imaginary roots $\lambda_{1,2}=\pm i\omega$, where

$$\omega^2=\alpha\gamma+\frac{2\alpha\sigma(\rho+\sigma)}{r+s},$$

and a pair of roots $\lambda_{3,4}$ with negative real parts, so the frequency ω of the oscillating components of the solution in the neighborhood of equilibrium (in the linear approximation) exceeds the frequency of oscillations in the isolated subsystem.

Thus, when migration with the intensity which varies with the direction on both levels preserves identical equilibrium values $\overset{*}{x}{}^1=\overset{*}{x}{}^2$ for the two subsystems on the prey level, it stabilizes the equilibrium for all admissible values of the model parameters, and when the same population is preserved on the predator level, the stabilizing effect of migration shows up under the additional restriction (8.42).

On the whole, from the results of this section (though the considered examples were specially chosen and limited by the linear description of migration flows) we still can infer that the stabilizing effect of migration upon the community dynamics is far from being unambiguous. Recall that the schemes of the present and preceding sections also presupposed identity of equations for biological interactions within the subsystems. A more general (from this standpoint) formulation of the problem is considered in the following section; however, it assumes that the migration parameters are sufficiently small as compared with the parameters of biological interactions.

8.5. Small parameter method in studies of migration effects

Let n, generally speaking, different habitats (but with the same collection of p species) be linked together by some migration pattern. The community dynamics within the kth isolated system is characerized by the system of equations

$$\frac{dN_i^k}{dt}=f_i^k(N_1^k,\ldots,N_p^k),\qquad i=1,\ldots,p, \quad (8.43)$$

or in the vector form

$$\frac{d\mathbf{N}^k}{dt}=\mathbf{F}^k(\mathbf{N}^k), \quad (8.43')$$

where the p-vectors are

$$\mathbf{N}^k = [N_1^k, \ldots, N_p^k], \qquad \mathbf{F}^k(\mathbf{N}) = [f_1^k(\mathbf{N}), \ldots, f_p^k(\mathbf{N})].$$

As before, concerning the biological interactions within the community it will only be assumed that they are represented by sufficiently smooth functions f_i^k (which are generally different for different subsystems) with the non-trivial equilibrium $\overset{*}{\mathbf{N}}{}^k$.

Suppose also that the migration process is governed by some functions m_i^{ks} —the instantaneous intensities of the ith species migration on the route from the sth to the kth habitat—which depend (in the very general case) upon the populations of all species in all subsystems:

$$m_i^{ks} = m_i^{ks}(\mathbf{N}^1, \ldots, \mathbf{N}^n), \qquad i = 1, \ldots, p; \qquad k, s = 1, \ldots, n. \tag{8.44}$$

Then the migration effect on the variations in the ith species, say, in the first subsystem, manifests itself as the input of immigrants into the given subsystem

$$\sum_{\substack{s=1\\ s\neq 1}}^{n} N_i^s m_i^{1s}$$

and the outflow of emigrants from this subsystem to all the rest

$$\sum_{\substack{s=1\\ s\neq 1}}^{n} N_i^1 m_i^{s1}.$$

Equations (8.43) then take the form

$$\frac{dN_i^k}{dt} = f_i^k(N_1^k, \ldots, N_p^k) + \sum_{\substack{s=1\\ s\neq k}}^{n} (N_i^s m_i^{ks} - N_i^k m_i^{sk}), \tag{8.45}$$

and if we denote by $\mathbf{z} = [\mathbf{N}^1, \ldots, \mathbf{N}^n]$ the np-vector, which specifies the state of all the n linked subsystems, then the dynamic equations for the united system may be written in their vector form as

$$\frac{d\mathbf{z}}{dt} = \mathbf{F}(\mathbf{z}) + \mathbf{M}(\mathbf{z}). \tag{8.46}$$

Here the vector-function $\mathbf{F}(\mathbf{z})$ characterizes the biological interactions within the subsystems and, clearly,

$$\mathbf{F}(\mathbf{z}) = [\mathbf{F}^1(\mathbf{N}^1), \ldots, \mathbf{F}^n(\mathbf{N}^n)],$$

and the vector-function $\mathbf{M}(\mathbf{z})$ determines the structure of migration links and their effect on the population dynamics. In the adopted

notations

$$\mathbf{M}(\mathbf{z}) = \Big[\sum_{s=2}^{n} (N_1^s m_1^{1s}(\mathbf{z}) - N_1^1 m_1^{s1}(\mathbf{z})), \ldots, \sum_{s=2}^{n} (N_p^s m_p^{1s}(\mathbf{z}) - N_p^1 m_p^{s1}(\mathbf{z})), \ldots, \sum_{s=1}^{n-1} (N_1^s m_1^{ns}(\mathbf{z}) - (N_1^n m_1^{sn}(\mathbf{z})), \ldots, \sum_{s=1}^{n-1} (N_p^s m_p^{ns}(\mathbf{z}) - N_p^n m_p^{sn}(\mathbf{z}))\Big]. \quad (8.47)$$

Rejecting the rather unrealistic assumption about isotropy of the environment with respect to the migration flows, and also the constancy of the functions $m_i^{hs}(\mathbf{z})$ (which was the case in Section 8.3), on the other hand, we now will think that the migration processes influence the state of the system far less, than the basic biological interactions. Mathematically, this assumption is expressed by the introduction of a small parameter $\varepsilon > 0$ into the right-hand side of the system (8.46):

$$\frac{d\mathbf{z}}{dt} = \mathbf{F}(\mathbf{z}) + \varepsilon \mathbf{M}(\mathbf{z}). \quad (8.48)$$

Can we state that for all sufficiently small values of ε a non-trivial equilibrium $\mathbf{z}^*(\varepsilon)$ is possible in this system? When $\varepsilon = 0$ the migration links vanish and the system disintegrates into n isolated subsystems; it is natural to denote the set of equilibriums $\overset{*}{\mathbf{N}}{}^h$ in these subsystems by

$$\mathbf{z}^*(0) = [\overset{*}{\mathbf{N}}{}^1, \ldots, \overset{*}{\mathbf{N}}{}^n].$$

It turns out that for small $\varepsilon > 0$ the equilibrium $\mathbf{z}^*(\varepsilon)$ also exists.

In fact, consider the mapping $\varphi\left[\frac{\mathbf{z}}{\varepsilon}\right] = \mathbf{F}(\mathbf{z}) + \varepsilon \mathbf{M}(\mathbf{z})$ which transfers a certain neighborhood of the point $\begin{bmatrix} \mathbf{z}^*(0) \\ 0 \end{bmatrix}$ in the coordinate space R^{np+1} into the space R^{np}. Under the assumption about the functions $\mathbf{F}(\mathbf{z})$ and $\mathbf{M}(\mathbf{z})$ being sufficiently smooth, the mapping φ and its partial derivatives are continuous in all the arguments. Besides, according to the definition of equilibrium points

$$\varphi\begin{bmatrix} \mathbf{z}^*(0) \\ 0 \end{bmatrix} = 0,$$

and we require for the Jacoby matrix of the multivariate function φ, calculated at the point $\begin{bmatrix} \mathbf{z}^*(0) \\ 0 \end{bmatrix}$ by the formula

$$J = J(\mathbf{z}^*(0)) = \frac{\partial \varphi}{\partial \mathbf{z}}\Big|_{\begin{bmatrix} \mathbf{z}^*(0) \\ 0 \end{bmatrix}} = \frac{\partial \mathbf{F}(\mathbf{z})}{\partial \mathbf{z}}\Big|_{\mathbf{z}^*(0)}, \quad (8.49)$$

that it be non-singular. The latter is equivalent to non-singularity of matrices of all subsystems, linearized at their equilibrium points $\overset{*}{N}{}^1, \ldots, \overset{*}{N}{}^n$.

Now the implicit function theorem ensures that for each value of ε in an interval $-\delta < \varepsilon < \delta$, $\delta > 0$ there exists the function $z^*(\varepsilon)$ such that

$$\varphi \begin{bmatrix} z^*(\varepsilon) \\ \varepsilon \end{bmatrix} = 0,$$

i.e. $z^*(\varepsilon)$ proves to be an equilibrium for the system (8.48) and

$$z^*(\varepsilon) = z^*(0) - \varepsilon J^{-1} M(z^*(0)) + O(\varepsilon^2). \tag{8.50}$$

It follows that if the components of the previous equilibrium populations in the isolated subsystems were positive, then for small ε their positiveness is also preserved in the equilibrium $z^*(\varepsilon)$ for the united system.

Let us find the matrix $\mathcal{A}(\varepsilon)$ for the system (8.48) linearized at the point $z^*(\varepsilon)$, i.e. the matrix of the linear system

$$\dot{x} = \mathcal{A}(\varepsilon)\, x, \tag{8.51}$$

where $x(t) = z(t) - z^*(\varepsilon)$. By the general rule this matrix is

$$\mathcal{A}(\varepsilon) = \frac{\partial F(z)}{\partial z}\bigg|_{z^*(\varepsilon)} + \varepsilon \frac{\partial M(z)}{\partial z}\bigg|_{z^*(\varepsilon)}.$$

If the rsth elements of the matrices added here are denoted by $j_{rs}(z)$ and $d_{rs}(z)$, then the appropriate element in $\mathcal{A}(\varepsilon)$ is

$$a_{rs}(\varepsilon) = (j_{rs} + \varepsilon d_{rs})(z^*(\varepsilon)),$$

and expanding these functions into a Taylor series at the point $\varepsilon = 0$ gives

$$a_{rs}(z^*(\varepsilon)) = j_{rs}(z^*(0)) + \varepsilon \frac{d}{d\varepsilon} j_{rs}(z^*(\varepsilon))\big|_{\varepsilon=0} + \varepsilon d_{rs}(z^*(0)) + O(\varepsilon^2)$$

$$= (j_{rs} + \varepsilon d_{rs})(z^*(0)) + \varepsilon \frac{\partial j_{rs}(z)}{\partial z}\bigg|_{z^*(0)} \frac{dz^*(\varepsilon)}{d\varepsilon}\bigg|_{\varepsilon=0} + O(\varepsilon^2). \tag{8.52}$$

Here $\partial j_{rs}(z)/\partial z$ is the gradient of the function $j_{rs}(z)$ and it is a $1 \times \times np$ matrix, $dz^*(\varepsilon)/d\varepsilon$ is an np-column-vector, that by (8.50), is

$$\frac{dz^*(\varepsilon)}{d\varepsilon}\bigg|_{\varepsilon=0} = -J^{-1} M(z^*(0)).$$

Consequently, the sought matrix $\mathcal{A}$ has the form

$$\mathcal{A}(\varepsilon) = J + \varepsilon \left[\frac{\partial M(z)}{\partial z}\bigg|_{z^*(0)} - H \right] + O(\varepsilon^2), \tag{8.53}$$

where matrix H is built of elements

$$h_{rs} = \frac{\partial j_{rs}(z)}{\partial z}\bigg|_{z^*(0)} \cdot J^{-1} M(z^*(0)); \quad r, s = 1, \ldots, np. \tag{8.54}$$

The well-known principle of the small parameter method states, that if all the eigenvalues $\lambda_1, \ldots, \lambda_{np}$ of matrix J are mutually different, the eigenvalues of matrix $\mathcal{A}(\varepsilon) = J + \varepsilon E + O(\varepsilon^2)$ may be represented in the form

$$\lambda_i(\varepsilon) = \lambda_i + \varepsilon\lambda_i^{(1)} + O(\varepsilon^2), \qquad i = 1, \ldots, np, \tag{8.55}$$

with the coefficient at ε expressed in terms of the scalar product

$$\lambda_i^{(1)} = (\mathbf{u}_i, E\mathbf{v}_i), \tag{8.56}$$

where $\{\mathbf{v}_1, \ldots, \mathbf{v}_{np}\}$ is a normalized system of eigenvectors for J, and $\{\mathbf{u}_1, \ldots, \mathbf{u}_{np}\}$ is a normalized system of eigenvectors for the Hermitian-conjugate matrix J^H, associated with the complex conjugate values $\{\bar{\lambda}_1, \ldots, \bar{\lambda}_{np}\}$.

It should be noted that the schemes examined in the preceding section did not satisfy the restrictions of this method, because the spectrum of matrix J, formed by the union of spectra of isolated subsystems, was made up of n similar collections.

Based on the estimate (8.55) the definitions for the *stabilizing effect* of migration and for the *equilibrium-stabilizing* migration pattern may be given in a natural way. We shall say that migration according to the pattern $\mathbf{M}(\mathbf{z})$ has a *stabilizing effect* (or shows a *stabilizing trend*) if for all the coefficients $\lambda_i^{(1)}\mathrm{Re}\,\lambda_i^{(1)} < 0$, $i = 1, \ldots, \ldots, np$, i.e. the real parts of eigenvalues in the united system are reduced as compared with those in the isolated subsystems. The migration pattern $\mathbf{M}(\mathbf{z})$ will be termed *equilibrium-stabilizing* at the point $\mathbf{z}^*(0)$, if the equilibrium $\mathbf{z}^*(0)$ of the system (8.48) for $\varepsilon = 0$ does not feature asymptotic stability, whereas for all sufficiently small ε, $0 < \varepsilon < \delta$, the equilibrium $\mathbf{z}^*(\varepsilon)$ is asymptotically stable. Clearly, this case is only possible when there are no eigenvalues $\lambda_i(0)$ with positive real parts and $\mathrm{Re}\,\lambda_i(\varepsilon) < 0$, $i = 1, \ldots, np$, i.e. migration in this case improves the stability properties of equilibrium, replacing neutral stability of $\mathbf{z}^*(0)$ by asymptotic stability of $\mathbf{z}^*(\varepsilon)$.

From (8.56) to see whether or not the migration pattern $\mathbf{M}(\mathbf{z})$ has a stabilizing effect on community dynamics and whether $\mathbf{M}(\mathbf{z})$ produces an asymptotically stable equilibrium $\mathbf{z}^*(\varepsilon)$, we, by (8.56), have to find the eigenvectors $\{\mathbf{u}_1, \ldots, \mathbf{u}_{np}\}$ and $\{\mathbf{v}_1, \ldots, \mathbf{v}_{np}\}$ for the matrix

$$J = \frac{\partial \mathbf{F}(\mathbf{z})}{\partial \mathbf{z}}\bigg|_{\mathbf{z}^*(0)} = \mathrm{diag}\{A_1(\overset{*}{\mathbf{N}}{}^1), \ldots, A_n(\overset{*}{\mathbf{N}}{}^n)\}, \tag{8.57}$$

where the $p \times p$ diagonal blocks $A_k(\overset{*}{\mathbf{N}}{}^k)$ are the matrices of isolated subsystems, linearized at their equilibrium point $\overset{*}{\mathbf{N}}{}^k$. The spectrum of J is thus composed of n different collections of eigenvalues $\alpha_1^k, \ldots \ldots, \alpha_p^k$ belonging to the matrices $A_k(\overset{*}{\mathbf{N}}{}^k)$, $k = 1, \ldots, n$, i.e. we

can set $\lambda_{(k-1)p+j} = \alpha_j^k$, $j = 1, \ldots, p$ in the expression (8.55). If at the same time $\{\mathbf{e}_1^k, \ldots, \mathbf{e}_p^k\}$ is a normalized system of eigenvalues (in p dimensions), belonging to the values $\alpha_1^k, \ldots, \alpha_p^k$, then the np-vectors

$$\begin{aligned}
&\mathbf{v}_{(k-1)p+1} = [0, \ldots, 0, \mathbf{e}_1^k, 0, \ldots, 0],\\
&\mathbf{v}_{(k-1)p+2} = [0, \ldots, 0, \mathbf{e}_2^k, 0, \ldots, 0],\\
&\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\\
&\mathbf{v}_{kp} = [0, \ldots, \mathbf{e}_p^k, 0, \ldots, 0], \quad k = 1, \ldots, n,
\end{aligned} \tag{8.58}$$

make up a normalized system of eigenvectors for matrix J. The system of vectors $\{\mathbf{u}_1, \ldots, \mathbf{u}_{np}\}$ is constructed in an analogous way. Next we can find the sign of the expression

$$\operatorname{Re} \lambda_i^{(1)} = \operatorname{Re} (\mathbf{u}_i, E\mathbf{v}_i),$$

where

$$E = \left.\frac{\partial \mathbf{M}(\mathbf{z})}{\partial \mathbf{z}}\right|_{\mathbf{z}^*(0)} - H, \tag{8.59}$$

and matrix H was defined in (8.54).

Example. Consider the migration between two predator-prey subsystems occurring on both levels. Modifying the system (8.37) of the preceding section in such a way that subsystems become different from one another, assume that

$$\begin{aligned}
&f_x^1(x, y) = x - xy, \qquad && f_x^2(x, y) = 2f_x^1(x, y);\\
&f_y^1(x, y) = -y + xy, && f_y^2(x, y) = 2f_y^1(x, y).
\end{aligned}$$

Then the equation of the united community will take the form (with no restrictions on the signs of variables ρ and σ)

$$\begin{aligned}
\dot{x}^1 &= x^1 - x^1y^1 - (r-\rho)\, x^1 + (r+\rho)\, x^2,\\
\dot{y}^1 &= -y^1 + x^1y^1 - (s-\sigma)\, y^1 + (s+\sigma)\, y^2,\\
\dot{x}^2 &= 2(x^2 - x^2y^2) + (r-\rho)\, x^1 - (r+\rho)\, x^2,\\
\dot{y}^2 &= 2(-y^2 + x^2y^2) + (s-\sigma)\, y^1 - (s+\sigma)\, y^2,
\end{aligned} \qquad (r, s > 0) \tag{8.60}$$

where in the symbols of the present section

$$\mathbf{z} = \begin{bmatrix} x^1\\ y^1\\ x^2\\ y^2 \end{bmatrix}; \qquad \mathbf{M}(\mathbf{z}) = \begin{bmatrix} -(r-\rho)\, x^1 + (r+\rho)\, x^2\\ -(s-\sigma)\, y^1 + (s+\sigma)\, y^2\\ (r-\rho)\, x^1 + (r+\rho)\, x^2\\ (s-\sigma)\, y^1 - (s+\sigma)\, y^2 \end{bmatrix};$$

$$\frac{\partial \mathbf{F}(\mathbf{z})}{\partial \mathbf{z}} = \| j_{rs}(\mathbf{z}) \|$$

$$= \begin{Vmatrix} 1-y^1-(r-\rho) & -x^1 & r+\rho & 0 \\ y^1 & (x^1-1)-(s-\sigma) & 0 & s+\sigma \\ r-\rho & 0 & 2(1-y^2)-(r+\rho) & -2x^2 \\ 0 & s-\sigma & 2y^2 & 2(x^2-1)-(s+\sigma) \end{Vmatrix}.$$

Equilibria in isolated subsystems coincide: $\overset{*}{\mathbf{N}}{}^1 = \overset{*}{\mathbf{N}}{}^2 = [1, 1]^T$ so $\mathbf{z}^*(0) = [1, 1, 1, 1]^T$ and the appropriate matrices

$$A_1 = \begin{Vmatrix} 0 & -1 \\ 1 & 0 \end{Vmatrix}, \qquad A_2 = \begin{Vmatrix} 0 & -2 \\ 2 & 0 \end{Vmatrix}$$

give the set of eigenvalues for $J = \operatorname{diag}\{A_1, A_2\}$:

$$\{\lambda_1, \lambda_2, \lambda_3, \lambda_4\} = \{i, -i, 2i, -2i\},$$

and therefore the equilibrium $\mathbf{z}^*(0)$ is neutrally stable. The appropriate eigenvectors are

$$\mathbf{v}_1 = \mathbf{u}_1 = \frac{1}{\sqrt{2}} \begin{bmatrix} 1 \\ -i \\ 0 \\ 0 \end{bmatrix}, \qquad \mathbf{v}_2 = \mathbf{u}_2 = \frac{1}{\sqrt{2}} \begin{bmatrix} 1 \\ i \\ 0 \\ 0 \end{bmatrix},$$

$$\mathbf{v}_3 = \mathbf{u}_3 = \frac{1}{\sqrt{2}} \begin{bmatrix} 0 \\ 0 \\ 1 \\ -i \end{bmatrix}, \qquad \mathbf{v}_4 = \mathbf{u}_4 = \frac{1}{\sqrt{2}} \begin{bmatrix} 0 \\ 0 \\ 1 \\ i \end{bmatrix}.$$

Having calculated the vector

$$J^{-1}\mathbf{M}(\mathbf{z}^*(0)) = \left\| \begin{array}{cc|cc} 0 & 1 & \multicolumn{2}{c}{0} \\ -1 & 0 & & \\ \hline \multicolumn{2}{c|}{0} & 0 & 1/2 \\ & & -1/2 & 0 \end{array} \right\| \begin{bmatrix} 2\rho \\ 2\sigma \\ -2\rho \\ -2\sigma \end{bmatrix} = -\begin{bmatrix} 2\sigma \\ -2\rho \\ -\sigma \\ \rho \end{bmatrix},$$

we find the equilibrium (8.50) in the united system

$$\mathbf{z}^*(\varepsilon) = \begin{bmatrix} 1-\varepsilon 2\sigma \\ 1+\varepsilon 2\rho \\ 1+\varepsilon\sigma \\ 1-\varepsilon\rho \end{bmatrix} + O(\varepsilon^2),$$

whence the effect of distinctions in migration intensities on the alteration of equilibrium populations becomes evident.

Next, in order to determine the matrix (8.59) we find

$$\left.\frac{\partial \mathbf{M}(\mathbf{z})}{\partial \mathbf{z}}\right|_{\mathbf{z}^*(0)} = \begin{Vmatrix} -(r-\rho) & 0 & r+\rho & 0 \\ 0 & -(s-\sigma) & 0 & s+\sigma \\ r-\rho & 0 & -(r+\rho) & 0 \\ 0 & s-\sigma & 0 & -(s+\sigma) \end{Vmatrix};$$

the gradients for elements of the matrix $\partial \mathbf{F}/\partial \mathbf{z}$ calculated at the point $\mathbf{z}^*(0)$ are

$$\partial j_{11}/\partial \mathbf{z} = [0,\ -1,\ 0,\ 0], \qquad \partial j_{12}/\partial \mathbf{z} = [-1,\ 0,\ 0,\ 0],$$
$$\partial j_{21}/\partial \mathbf{z} = [0,\ 1,\ 0,\ 0], \qquad \partial j_{22}/\partial \mathbf{z} = [1,\ 0,\ 0,\ 0],$$
$$\partial j_{33}/\partial \mathbf{z} = [0,\ 0,\ 0,\ -2], \qquad \partial j_{34}/\partial \mathbf{z} = [0,\ 0,\ -2,\ 0],$$
$$\partial j_{43}/\partial \mathbf{z} = [0,\ 0,\ 0,\ 2], \qquad \partial j_{44}/\partial \mathbf{z} = [0,\ 0,\ 2,\ 0],$$

and all the rest $\partial j_{rs}/d\mathbf{z}$ are zero. In consequence, according to (8.54),

$$H = \begin{Vmatrix} 2\rho & -2\sigma & 0 & 0 \\ -2\rho & 2\sigma & 0 & 0 \\ 0 & 0 & -2\rho & 2\sigma \\ 0 & 0 & 2\rho & -2\sigma \end{Vmatrix},$$

hence

$$E = \begin{Vmatrix} -(r+\rho) & 2\sigma & r+\rho & 0 \\ 2\rho & -(s+\sigma) & 0 & s+\sigma \\ r-\rho & 0 & -(r-\rho) & -2\sigma \\ 0 & s-\sigma & -2\rho & -(s-\sigma) \end{Vmatrix}.$$

Now the coefficients for ε in the estimate (8.55), calculated in the form $\lambda_j^{(1)} = (\mathbf{u}_j,\ E\mathbf{v}_j)$ are

$$\lambda_{1,2}^{(1)} = \frac{1}{2}\,[-(r+\rho)-(s+\sigma)] \mp i\,(\rho+\sigma);$$

$$\lambda_{3,4}^{(1)} = \frac{1}{2}\,[-(r-\rho)-(s-\sigma)] \mp i\,(\rho+\sigma).$$

Thus, if $(r+\rho)+(s+\sigma) > 0$ and $(r-\rho)+(s-\sigma) > 0$, then for sufficiently small ε the equilibrium $\mathbf{z}^*(\varepsilon)$ is asymptotically stable. Therefore, if at least one of the species migrates from habitat 2 into habitat 1 and, at least, one of the species from 1 into 2, then the considered migration pattern $\mathbf{M}(\mathbf{z})$ is equilibrium-stabilizing at the point $\mathbf{z}^*(0) = [1,\ 1,\ 1,\ 1]$ for the interaction (8.60).

8.6. Diffusion models of spatially distributed communities. Occurrence of diffusive instability

In the foregoing chapters we have investigated community models with dynamics identical for all the points in the space occupied by the community or ecosystem, and naturally for their description it was fairly sufficient to use the system of ordinary differential equations

$$\frac{dN_i}{dt} = f_i(N_1, \ldots, N_n; \alpha_1, \ldots, \alpha_s), \qquad i = 1, \ldots, n, \tag{8.61}$$

where N_i is the number (or density) of species in the community, and $\alpha_1, \ldots, \alpha_s$ are parameters common for all the points in space. And it is only in the present chapter that we started to examine spatially distributed communities, but still using ordinary differential equations, as in the model of phytoplankton vertical distribution or in models of communities linked by migration. However, models, which use the techniques of partial differential equations, have been developed long enough. While the reasoning in the previous sections implied the presence of "point" communities with migration between "points", the alternate situation takes place when the radii of individual activity of specimens are small as compared with the sizes of the areal occupied by the community. If the species migration (within the space of one habitat) is of a random origin and is equiprobable in direction, then the description by diffusion equations becomes adequate, thus the spatial analog for the model (8.61) takes the form

$$\frac{\partial N_i}{\partial t} = D_i \Delta N_i + f_i, \qquad i = 1, \ldots, n. \tag{8.62}$$

Here $N_i = N_i(x, y, t)$ is the density of specimens at the point (x, y) (it is natural to consider the two-dimensional areal for these problems), $\Delta = d^2/dx^2 + \partial^2/\partial y^2$ is the Laplace operator, and the diffusion coefficient $D_i > 0$ is a variable proportional to the square of the radius of individual activity for a specimen of the ith species.

If we suppose that there exists a stationary solution to (8.62) that is uniform in space, then it should satisfy the equations

$$f_i(N_1^*, \ldots, N_n^*) = 0, \qquad i = 1, \ldots, n \tag{8.63}$$

(the parameters α_s are identical for all the points in space).

To study stability of the solution $\mathbf{N}^* = [N_1^*, \ldots, N_n^*]$ linearize the system (8.62) in the neighborhood of this solution:

$$\frac{\partial n_i}{\partial t} = D_i \Delta n_i + \sum_{j=1}^{n} a_{ij} n_j, \qquad i = 1, \ldots, n. \tag{8.64}$$

Here $n_i = n_i(x, y, t) = N_i(x, y, t) - N_i^*$, $a_{ij} = \partial f_i/\partial N_j \,|_{\mathbf{N}^*}$.

Let us seek the solution to (8.64) in the form

$$n_i(x, y, t) = \tilde{n}_i \cos(k_1 x + k_2 y + \theta) \exp\{\varkappa t\}, \tag{8.65}$$

where $\tilde{n}_i$, k_1, k_2, θ and $\varkappa$ are constants. This form of solution enables one to satisfy a fairly broad class of initial conditions (all the functions which allow a Fourier-series expansion). Inserting (8.65) into (8.64) we get the relationships between these constants:

$$\sum_{j=1}^{n} [a_{ij} - (\varkappa + D_i k^2)\,\delta_{ij}]\,\tilde{n}_i = 0, \qquad i = 1, \ldots, n, \tag{8.66}$$

where

$$k^2 = k_1^2 + k_2^2, \qquad \delta_{ij} = \begin{cases} 1, & i = j, \\ 0, & i \neq j. \end{cases}$$

The equilibrium $\mathbf{N}^* = [N_1^*, \ldots, N_n^*]$ will be asymptotically stable if and only if $\operatorname{Re} \varkappa < 0$. On the other hand, as it follows from (8.66), the values of $\varkappa$ are to be eigenvalues for the matrix $\| a_{ij} - D_i k^2 \delta_{ij} \|$, so that the problem of the equilibrium stability with respect to perturbation of the (8.65) type is reduced to the localization of these eigenvalues. And the problem of equilibrium stability at every point in space in the absence of diffusion, in other words, the problem of *local stability*, is concerned with the analysis of eigenvalues for matrix $\| a_{ij} \|$).

Let all $\operatorname{Re} \lambda_i$ ($\| a_{ij} \|$) be negative, i.e. in the absence of diffusion the equilibrium $[N_1^*, \ldots, N_n^*]$ is asymptotically stable. But if $D_i \neq 0$, it is not improbable that with certain values of the wave number k (it is readily seen that $2\pi/k$ is the spatial period of perturbations) the matrix $\| a_{ij} - D_i k^2 \delta_{ij} \|$ will produce an eigenvalue with a positive real part, and the amplitude of all perturbations with these wave numbers will grow, i.e., a typical phenomenon of instability develops. Instability of this kind will be termed *diffusive*. The reverse effect is also possible, diffusion may stabilize the system and a locally unstable equilibrium under the effect of diffusive intermixing may give rise to *diffusive stability* (i.e. against perturbations with certain wave numbers).

Consider some examples. Suppose all species in the community have identical mobility characteristics, that is, $D_i = D$. Then if λ_i are the eigenvalues of $\| a_{ij} \|$ and $\varkappa_i$ are the eigenvalues of $\| a_{ij} - Dk^2 \delta_{ij} \|$, then

$$\lambda_i = \varkappa_i + Dk^2, \qquad i = 1, \ldots, n. \tag{8.67}$$

It follows immediately that if all $\operatorname{Re} \lambda_i$ are negative, then $\operatorname{Re} \varkappa_i$ are all the more negative, i.e. if the equilibrium is locally stable, the diffusive intermixing only improves the stability of this equilibrium. Suppose now some λ_p has a $\operatorname{Re} \lambda_p = \zeta_p > 0$, i.e. the local

equilibrium is unstable. If $\zeta_p = \max \operatorname{Re} \lambda_i$, then obviously this equilibrium will demonstrate stability (diffusive) with respect to spatial perturbations with wave numbers $k > k_p^\circ = \sqrt{\zeta_p/D}$. It follows that diffusion is most effective in damping short-period spatial perturbations.

It should be noted that since the spatial equilibrium distribution is homogeneous, it fits the local equilibrium at every point, and only for this reason we can speak about the stabilization of the local equilibrium. Here we find an analogy with the model of "point" migration in isotropic medium, where identical equilibria pertained to all the "points" (Section 8.3). Diffusive stability of a local equilibrium implies nothing but the stability of a homogeneous spatial equilibrium with respect to periodic spatial perturbations.

8.7. Occurrence of diffusive instability in predator-prey type systems

Let the local interaction between populations of the prey (N_1) and the predator (N_2) be characterized by the system of two ordinary differential equations

$$dN_1/dt = f_1(N_1, N_2), \qquad dN_2/dt = f_2(N_1, N_2), \tag{8.68}$$

which has a positive steady-state solution $[N_1^*, N_2^*]$. This solution is stable if the real parts of eigenvalues for the matrix

$$A = \begin{Vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{Vmatrix}, \qquad a_{ij} = \frac{\partial f_i}{\partial N_j}\Big|_{[N_1^*,\, N_2^*]}, \qquad i = 1,\ 2,$$

are negative. And this is so if and only if

$$a_{11} + a_{22} < 0, \qquad a_{11}a_{22} - a_{12}a_{21} > 0. \tag{8.69}$$

The necessary and sufficient condition for diffusive instability to develop is the presence of at least one eigenvalue with a positive real part in the spectrum of the matrix

$$A_D = \begin{Vmatrix} a_{11} - D_1k^2 & a_{12} \\ a_{21} & a_{22} - D_2k^2 \end{Vmatrix}.$$

This will happen if at least one of the conditions in (8.69) is not satisfied for the matrix A_D. Evidently, the first one is always satisfied, therefore, the polynomial

$$K(k^2) = D_1D_2k^4 - (D_1a_{22} + D_2a_{11})\,k^2 + a_{11}a_{22} - a_{21}a_{12}$$

need be negative for some k^2. The necessary condition for $K(k^2)$ to be negative is the inequality

$$D_1a_{22} + D_2a_{11} > 0, \tag{8.70}$$

whence it follows that at least one of the spacies should be self-stimulating.

It is easily seen that $K(k^2)$ has a minimum at the point

$$k^2_{\min} = \frac{D_1 a_{22} + D_2 a_{11}}{2D_1 D_2}, \tag{8.71}$$

which is equal to

$$K_{\min} = (a_{11}a_{22} - a_{12}a_{21}) - \frac{(D_1 a_{22} + D_2 a_{11})^2}{4D_1 D_2}. \tag{8.72}$$

The condition $K_{\min} < 0$ determines the possibility that diffusive instability will develop. Based on (8.69) and (8.70), the condition $K_{\min} < 0$ may be written in the form

$$D_1 a_{22} + D_2 a_{11} > 2\sqrt{D_1 D_2 (a_{11}a_{22} - a_{12}a_{21})}. \tag{8.73}$$

Suppose the system parameters fit the inequality which is opposite to (8.73) and in addition fit the inequalities (8.69). Then whatever the spatial perturbations, the local equilibria will be stable, and the uniform steady-state distribution for the prey and the predator populations will be preserved in the space. Suppose the system parameters are now slowly varied and at a particular moment in time the inequality (8.73) becomes satisfied with the inequalities (8.69) still valid. Then if there are oscillations with the wave number $k^2_{\min}$ in the spectrum of spatial perturbations, then their amplitude begins to grow, diffusive instability develops, the distribution ceases to be uniform and there appears a spatial periodic structure, i.e. a dissipative structure. Further development of this process may bring the originally united community to disintegration into separate disjoint cells.

In that case, though the local stability of equilibria is preserved, for $k_1^2 < k^2 < k_2^2$, where $k^2_{1,2}$ are determined from the equation $K(k^2) = 0$, they develop diffusive instability.

This reasoning may be illustrated by the example of a Volterra model with

$$f_1 = N_1(\varepsilon_1 - \gamma_{11}N_1 - \gamma_{12}N_2),$$
$$f_2 = N_2(-\varepsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2).$$

Since $a_{11} = -N_1^*\gamma_{11}$ and $a_{22} = -N_2^*\gamma_{22}$, satisfy the condition (8.70) is met at no $D_1, D_2 > 0$ when $\gamma_{ii} > 0$. For this reason let us consider a somewhat different model:

$$\begin{aligned} f_1 &= N_1(\varepsilon_1(N_1) - \gamma_{11}N_1 - \gamma_{12}N_2), \\ f_2 &= N_2(-\varepsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2), \end{aligned} \tag{8.74}$$

where

$$\varepsilon_1(N_1) = \frac{\alpha N_1}{1 + N_1}. \tag{8.75}$$

As $N_1 \to \infty$, $\varepsilon_1 \to \alpha$ and the model (8.74)-(8.75) coincides with the one of Volterra. But if N_1 is small then (in the absence of predator) $f_1 = \alpha N_1^2 - \gamma_{11} N_1^2$, i.e. the rate of the prey multiplication is in proportion to the square of its population. The latter adequately describes the case of bisexual multiplication, when the birth of new individuals essentially depends on the probability of formation of a reproductive pair.

Simplify the model, assuming that mortality resulting from intraspecial competition among the prey and the natural mortality of the predator (severe intraspecial competition) may be neglected. If, above all, we introduce new variables $\tau = \gamma_{12} t$, $\varepsilon = \alpha/\gamma_{12}$, $\gamma = \gamma_{22}/\gamma_{12}$ and assume that $\gamma_{12} = \gamma_{21}$, then the equations of the local model may be written in the form

$$\begin{aligned} \frac{dN_1}{d\tau} &= N_1 \left(\frac{\varepsilon N_1}{1+N_1} - N_2 \right), \\ \frac{dN_2}{d\tau} &= N_2 (N_1 - \gamma N_2). \end{aligned} \tag{8.76}$$

The non-trivial equilibrium has coordinates $N_1^* = \varepsilon\gamma - 1$, $N_2^* = (\varepsilon\gamma - 1)/\gamma$. Obviously, when $\varepsilon\gamma > 1$, N_1^*, N_2^* are positive. Calculating a_{ij} we get

$$a_{11} = N_2^*/\varepsilon\gamma, \qquad a_{22} = \gamma N_2^*, \qquad a_{12} = -\gamma N_2^*, \qquad a_{21} = N_2^*.$$

Inserting these values into (8.69), we get

$$\begin{aligned} a_{11} + a_{22} &= N_2^* \left(\frac{1}{\varepsilon\gamma} - \gamma \right) < 0, \\ a_{11}a_{22} - a_{12}a_{21} &= N_2^{*2} \left(\gamma - \frac{1}{\varepsilon} \right) > 0, \end{aligned} \tag{8.77}$$

i.e. with $\varepsilon\gamma^2 > 1$ and $\varepsilon\gamma > 1$ the local equilibrium is stable. Since N_1^*, $N_2^* > 0$ the second inequality in (8.77) always holds. And eventually, substituting for a_{ij} in (8.73), we obtain the condition for diffusive instability in the form

$$D_2 - D_1\varepsilon\gamma^2 > 2\gamma \sqrt{D_1 D_2 \varepsilon (\varepsilon\gamma - 1)}. \tag{8.78}$$

The critical wave number in this case will be

$$k_{\text{cr}}^2 = k_{\min}^2 = \frac{(D_2 - \varepsilon\gamma^2 D_1)(\varepsilon\gamma - 1)}{2\varepsilon\gamma^2 D_1 D_2}. \tag{8.79}$$

From (8.78) it is apparent, that if the predator mobility is much higher than the prey mobility (i.e. $D_2 \gg D_1$), then the inequality (8.78) will be certainly satisfied, and diffusive instability will develop. For a more graphic demonstration Fig. 50*a*, *b*, *c* gives the curves, which separate the domains of diffusive stability and instability (for three values of γ) in the plane of parameters $\delta = \sqrt{D_2/D_1}$ and ε. In Fig. 51 the relationship between k_{cr}^2 and δ

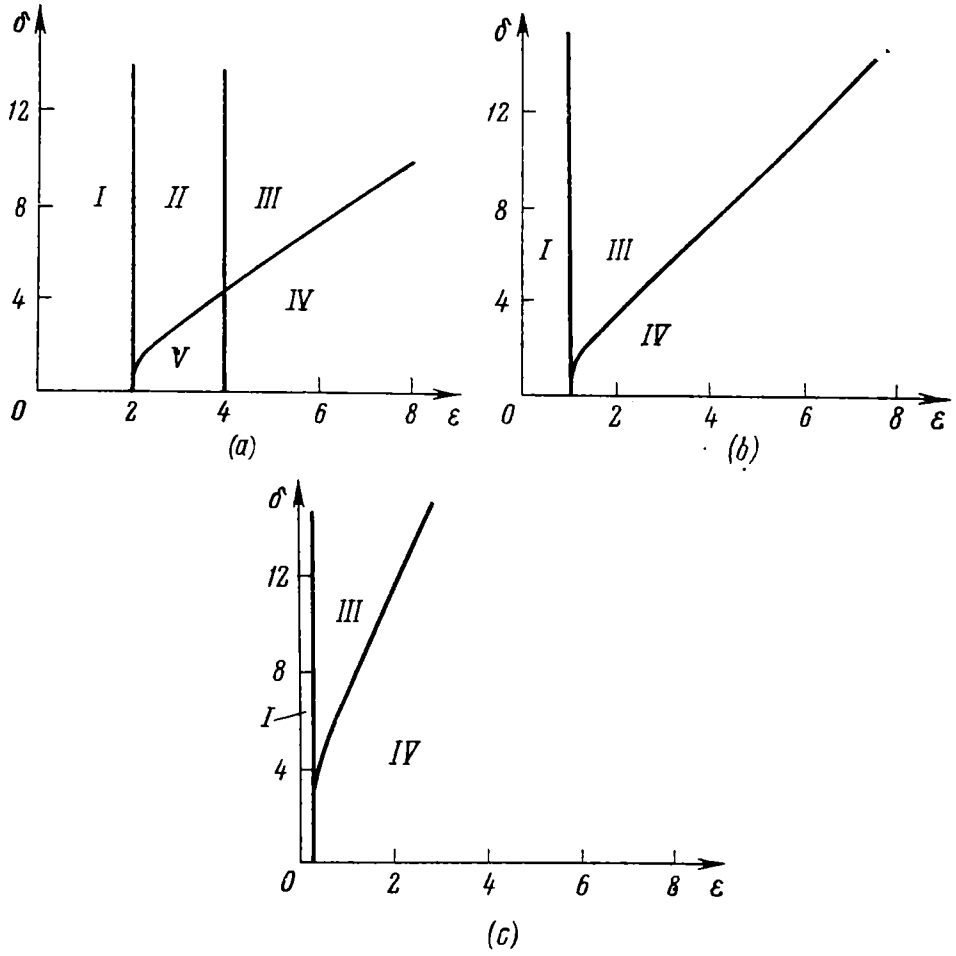

Fig. 50. Domains of different types of stability for several values of γ: (*a*) $\gamma = 0.5$, (*b*) $\gamma = 1$, (*c*) $\gamma = 5$. *I*—the system has no non-trivial equilibrium; *II*—there is an equilibrium, but it is unstable both locally and diffusively; *III*—the equilibrium is locally stable, but diffusively unstable, *IV*—the equilibrium is stable both locally and diffusively; *V*—the equilibrium is locally unstable but diffusively stable.

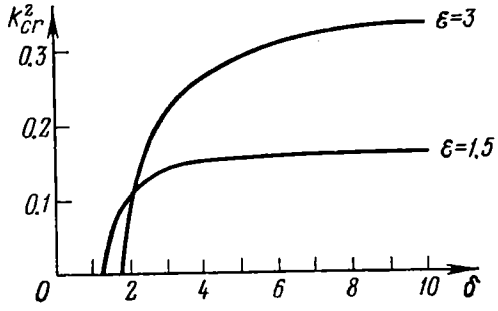

Fig. 51. The relationship between the critical wave number and the relation between radii of individual activity for the predator and the prey ($\gamma = 1$, $D_1 = 1$).

is illustrated (δ is proportional to the ratio of the individual activity radii for the predator and the prey).

These figures show that with the increase in ε (the natality coefficient of the prey) in order for the diffusive instability to develop, the mobility of the predator as compared with mobility of the prey is to increase as well. If the predator mobility is low, then for sure no diffusive instability will develop. The same effect is observed for the growth in γ—the coefficient of intraspecific competition among the predators. It is interesting that when $\gamma < 1$ (cf., for instance, Fig. 50*a*), there is a domain of values for ε and δ, in which the local equilibrium is unstable, but there exist such spatial perturbations (with certain periods), which stabilize these equilibria (diffusive stability). Thus the unstable local equilibria on the areal may develop a stable uniform distribution for the predator and the prey populations. The critical wave number (cf. Fig. 51) grows with δ, reaching a horizontal asymptote, the greater ε the higher the asymptote. These relationships indicate that at a high mobility of the predator and high fertility of the prey, most dangerous (from the standpoint of diffusive instability) are the short-period spatial perturbations.

8.8. Spatial structures in predator-prey system

In the preceding section it was shown that for certain values of the ratio between the predator and prey mobilities (diffusion coefficients) the stationary spatially homogeneous distributions of populations in the system lose stability. It is natural to expect that the loss of stability in these distributions will give rise to new stable stationary distributions, in a sense close to the former ones when the ratio $\mu = D_2/D_1$ is close enough to its critical value, but spatially non-homogeneous. Notice that these distributions must also provide solutions to the original system of partial differential equations.

This phenomenon really occurs: the so-called *spatial structures*, i.e. stationary spatially non-homogeneous stable solutions to system (8.62), are formed against the background of diffusive instability. The problem of their origination may be regarded as the problem of bifurcations in stationary solutions appearing when some parameter passes its critical value.

Only the simplest case of the spatial structure development will be looked at: suppose there are two equations in (8.62), the domain of definition Ω for the Laplace operator is limited, and the impermeability conditions are met on its boundary Γ, i.e. $\{\partial N_i/\partial \mathbf{n}\}\,|_\Gamma = 0$, $i = 1, 2$. The above ratio of diffusion coefficients $\mu = D_2/D_1$ is chosen as the bifurcation parameter.

If N_i^*, $i = 1, 2$ is the stationary solution to this system, then in its vicinity the system may be transformed into

$$\frac{\partial \mathbf{n}}{\partial t} = D(\mu)\,\Delta\mathbf{u} + A\mathbf{u} + \mathbf{g}(\mathbf{u}), \qquad \mathbf{u} = \mathbf{N} - \mathbf{N}^*, \tag{8.80}$$

with an appropriate change in the time-scale (or in the scale of spatial variables, as appropriate). Here

$$\mathbf{u} = \begin{vmatrix} u^1 \\ u^2 \end{vmatrix}, \qquad u^i = N_i - N_i^*, \qquad \mathbf{g} = \begin{vmatrix} g^1 \\ g^2 \end{vmatrix}, \qquad i = 1,\ 2;$$

$$D(\mu) = \begin{Vmatrix} 1 & 0 \\ 0 & \mu \end{Vmatrix}, \quad \mu > 0,$$

matrix A is the same as in the preceding section, $\mathbf{g}(\mathbf{u})$ is a small non-linear component, with $\mathbf{g}(0) = 0$. Accordingly the boundary conditions will be

$$\left\{\frac{\partial u^i}{\partial n}\right\}_\Gamma = 0, \qquad i = 1,\ 2. \tag{8.81}$$

Suppose that the parameter μ varies around some value μ_0, on passing this value the stability of the trivial solution $\mathbf{u} \equiv 0$ being replaced by instability. This means that an eigenvalue of one of the matrices $L_i(\mu) = D(\mu)\varkappa_i + A$ moves from the left complex half-plane to the right one. Here $\varkappa_0 = 0 > \varkappa_1 \geqslant \varkappa_2 \geqslant \ldots$ are the eigenvalues of the Laplace operator in the domain Ω; by $\varphi_i(x)$ we denote the eigenfunctions associated with them. In the simplest case this happens only for one $i = i_0 > 0$, the zero eigenvalue of $L_{i_0}(\mu_0)$ being simple, the eigenvalues of all the other matrices $L_i(\mu_0)$, $i \neq i_0$ lying inside the left half-plane. Then the following conditions imposed on A will be necessary for the origination of spatial structures:

$$\begin{aligned} &(1)\ \det A > 0, \qquad (2)\ a_{11} + a_{22} < 0, \\ &(3)\ a_{11} < 0 \quad \text{for} \quad a_{22} > 0, \quad \text{or} \quad a_{11} > |\varkappa_1|. \end{aligned} \tag{8.82}$$

The reader is encouraged to compare them with the conditions of diffusive instability in Section 8.7.

Notice that the conditions (8.82) are not only necessary, but they are almost always sufficient.

If the conditions (8.82) are met, then the solution to the equation

$$\det\{A + D(\mu)\varkappa\} = 0 \tag{8.83}$$

has the form

$$\mu(|\varkappa|) = \frac{1}{a_{11}}\left(\frac{a_{12}a_{21}}{|\varkappa| - a_{11}} + \frac{\det A}{|\varkappa|}\right). \tag{8.84}$$

The graphs of $\mu(|\varkappa|)$ with $a_{11} < 0$ and with $a_{11} > |\varkappa_1|$ are illustrated in Fig. 52*a*, *b* respectively. The point $(\mu_0, |\varkappa_{i_0}|)$ is to belong to the curve $\mu(|\varkappa|)$ and as it is extremal among all the points

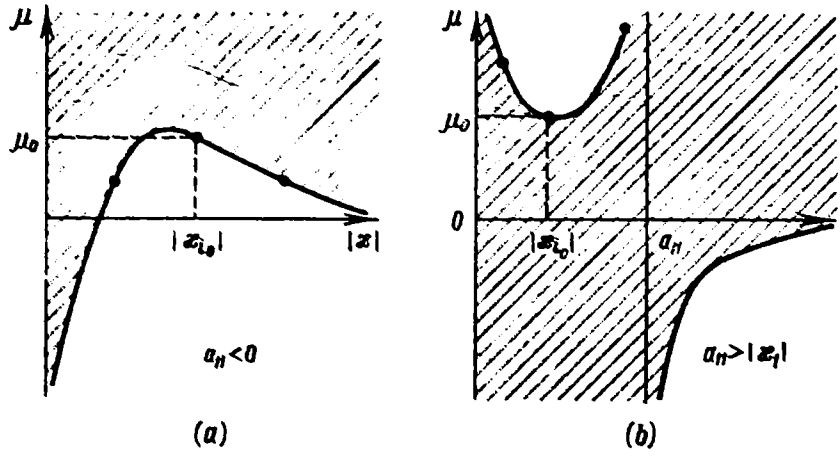

Fig. 52. The function $\mu(|\varkappa|)$—formulas (8.84). Points in the curves belong to $\varkappa_i$, the shaded domains belong to positive values of the determinant from (8.83).

$(\mu(|\varkappa_i|), \varkappa_i)$ with positive μ, it is to be found near the positive extremum of the curve $\mu(|\varkappa|)$. The corresponding value of $|\varkappa|_{\text{ext}}$ is equal to

$$|\varkappa|_{\text{ext}} = \frac{a_{11}}{1+\theta\sqrt{\omega}}, \qquad \omega = -\frac{a_{12}a_{21}}{\det A} > 1, \qquad \theta = \operatorname{sign} a_{11}.$$

Denote by $\hat{u}$ $(\hat{v})$ the eigenvectors of the matrix $L_{i_0}(\mu_0)$ $[L^T_{i_0}(\mu_0)]$ belonging to the zero eigenvalue of the operator $L(\mu_0)$. Let $\tilde{u}(x) = \hat{u}\varphi_{i_0}(x)$, $\tilde{v} = \hat{v}\varphi_{i_0}(x)$. Moreover, introduce the following notations:

$$g_{i_1\ldots i_r} = \left.\frac{\partial^r g}{\partial u^{i_1}\ldots\partial u^{i_r}}\right|_{u=0}, \qquad J_l = \int_\Omega \varphi^l_{i_0}(x)\,dx,$$

$$a = g^k_{ij}\hat{u}^i\hat{u}^j\hat{v}^k J_3.$$

(Here and in what follows it is implied that summation from 1 to 2 is performed over indices that occur twice.)

$$b = \varkappa_{i_0}\hat{u}^2\hat{v}^2 J_2, \qquad c = \hat{u}^i\hat{v}^i J_2.$$

If the conditions (8.82) are satisfied, then spatial inhomogeneous solutions of the original problem in the vicinity of the bifurcation

point may be sought in the form

$$\mathbf{u}(x, s) = s\hat{\mathbf{u}}(x) + o(s)$$

$$\mu(s) = \mu_0 + \alpha s + \frac{1}{2}\beta s^2 + o(s^2). \tag{8.85}$$

The small parameter s, introduced formally here, has also a biological meaning: the amplitude of spatial heterogeneities is of the order of $|s|$. Substituting the solution (8.85) into the equations (8.80) and the boundary conditions (8.81) and equating the terms of the same order in s, we get $\alpha = -a/2b$, $\beta = d/3b$. Computation of the magnitude of d involves the inversion of operator $L(\mu_0) = D(\mu_0)\Delta + A$ in the domain Ω and presents great difficulties. However, if the domain has a simple form (e.g. it is one-dimensional), the problem may be solved fairly simply. Thus, let Ω be a segment $[0, l]$ on the axis x, for example. Then $a = 0$, consequently $\alpha = 0$ and

$$d = \frac{3}{8} l \left(-g^p_{ijk}\hat{u}^i\hat{u}^j\hat{u}^k\hat{v}^p + \langle G(2A^{-1} + B)G\hat{\mathbf{u}}, \hat{\mathbf{v}}\rangle\right).$$

Here A^{-1} is the reciprocal matrix for A, G is the matrix with $g^k_{ij}\hat{u}^i$ as its kjth element, $B = (A - 4D(\mu_0)k_0^2)^{-1}$, $k_0 = li_0/\pi$; the symbol $\langle\ldots\rangle$ stands for the scalar product, so $\langle \mathbf{a}, \mathbf{b}\rangle = a^i b^i$.

These spatially inhomogeneous solutions will be stable for those μ for which the trivial solution features diffusive instability, and vice versa. Thus, for instance, when $a \neq 0$ and $\mu = \mu_0 + \alpha s + o(s)$, stable spatial structure will belong to negative values of as/c. But if $a = 0$ and $\mu = \mu_0 + \frac{1}{2}\beta s^2 + o(s^2)$ the similar result will take place for negative d/c, regardless of the sign of s.

As an application of the foregoing results consider the origination of spatial structures in a predator-prey system distributed over a finite one-dimensional areal of length l. Let the local interaction in this system be characterized by the relationships of (8.78). Denoting $l^2/\pi^2 D_1 = \sigma$, after the change of variables $x' = x\pi/l$, $t' = t/\sigma$ we shall again use the symbols x and t for the new variables. As in the preceding section, suppose $\varepsilon\gamma > 1$, $\varepsilon\gamma^2 > 1$ so the non-trivial spatially homogeneous equilibrium (N_1^*, N_2^*) is positive and locally stable.

Consider the system for deviations (8.80) with the boundary conditions (8.81) for this particular form of local interaction functions. Evidently, the coefficients of A will differ from those obtained in Section 8.7 by the factor σ. Then the conditions (8.82) will be met if $\varepsilon\gamma(\sigma - \gamma) > \sigma$. This inequality obviously always holds for $0 < \gamma < \sigma$ and large enough ε. In what follows γ will be considered a finite variable, ε and σ will be considered large, this conventionally represented by

$$\gamma \sim 1, \qquad \varepsilon, \sigma, \to +\infty. \tag{8.86}$$

In ecological terms the conditions (8.86) indicate that the prey population is very strongly influenced by mechanisms of intraspecific population regulation (as compared with the effect of the predator). Besides, as $\sigma \sim l^2/\rho_1$, where ρ_1 is the radius of the prey individual activity ($D_1 = \rho_1^2/4$), this radius is considered small compared with the areal dimensions, i.e. the prey is of low mobility.

We shall use the symbol $\simeq$ to distinguish the principal terms with respect to the independent parameters ε and $\varkappa$. In this case $a_{11} \simeq \varkappa/\gamma$, $a_{12} = a_{22} \simeq -\varkappa\varepsilon\gamma$, $a_{21} \simeq \varkappa\varepsilon$. Then the expression for $\mu(|\varkappa|)$ in (8.84) may be written in the form (the eigenvalues for the Laplace operator over a segment are simply i^2, which is the square of this eigenvalue number):

$$\mu(i^2) \simeq \frac{\sigma^2\varepsilon^2\gamma}{i^2(\sigma/\gamma - i^2)}$$

and takes on its minimal value, $\mu_0 \simeq 4\varepsilon^2\gamma^2$, for $i_0^2 \simeq \sigma/2\gamma$. Next, we find

$$L_0 \simeq \varkappa \begin{pmatrix} 0.5\gamma^{-1} & -\varepsilon\gamma \\ \varepsilon & -2\varepsilon^2\gamma^2 \end{pmatrix},$$

$$2B_0 + B_2 \simeq \frac{1}{9\sigma\varepsilon} \begin{pmatrix} -8\varepsilon\gamma & -19\gamma^{-1} \\ 19 & 17\varepsilon^{-1}\gamma^{-2} \end{pmatrix},$$

$$\hat{\mathbf{u}} = \begin{pmatrix} 1 \\ p \end{pmatrix}, \qquad \hat{\mathbf{v}} = \begin{pmatrix} 1 \\ q \end{pmatrix},$$

where $p \simeq 0.5\varepsilon^{-1}\gamma^{-2}$, $q \simeq -0.5\varepsilon^{-1}\gamma^{-1}$. Calculating the partial derivatives for $\mathbf{g}(\mathbf{u})$ we get:

$$\| g_{ij}^1 \| = \varkappa \begin{pmatrix} 2\gamma^{-3}\varepsilon^{-2} & -1 \\ -1 & 0 \end{pmatrix}, \qquad \| g_{ij}^2 \| = \sigma \begin{pmatrix} 0 & -1 \\ 1 & 2\gamma \end{pmatrix},$$

whence

$$G \simeq \sigma \begin{pmatrix} -p & -1 \\ p & 1 \end{pmatrix}.$$

Among the third derivatives only $g'_{111} = -\frac{6\sigma}{\varepsilon^3\gamma^4} = -\eta$ is nonzero, and so $g_{ijk}\hat{u}^i\hat{u}^j\hat{u}^k = (-\eta, 0)$.

Inserting the relations obtained into the expression for d, we find that the term, which incorporates the third derivatives, is negligibly small as compared with the other summands, therefore $d \simeq c\,\frac{\sigma r}{\varepsilon^2\gamma^2}$, $r = -4/\gamma + 19$. As in this case the variable c is always positive, it is necessary and sufficient for stability of spatial structures that $\gamma > 4/19$.

This result may find the following interpretation. Suppose $l \gg \rho_1$, $\varepsilon \gg 1$ and $\gamma > 4/19$, i.e. the prey is of low mobility, high fertility and with a rather strong intrapopulational regulation. Then one may find a ratio of mobilities D_2/D_1 close to but higher than $4\varepsilon^2\gamma^3$, such that any arbitrarily small spatially non-homogeneous perturbation will destroy the homogeneous distributions of the prey and the predator populations, and replace them by stable non-homogeneous stationary distributions of populations—the spatial structures.

For any small s ($|s|$ is equal in magnitude to the amplitude of spatial perturbations) these structures will be described by expressions

$$N_1^*(x) = (\varepsilon\gamma - 1) + s\varepsilon \cos\frac{\pi i_0}{l}\, x + o(s), \tag{8.87}$$

$$N_2^*(x) = \varepsilon - \frac{1}{\tau} + \frac{s}{2\gamma^2}\cos\frac{\pi i_0}{l}\, x + o(s),$$

where

$$i_0 = \frac{l}{\pi}\sqrt{\frac{1}{2D_1\gamma}} = \frac{l}{\pi\rho_1}\sqrt{\frac{2}{\gamma}}.$$

It is apparent that the period length, characterizing the spatial heterogeneity of the derived solutions, is $2\pi\rho_1\sqrt{\gamma/2}$, i.e. the emerging spatial structures are of a local character.

8.9. Populational waves

Let the population with its local dynamics specified by the equation $dN/dt = F(N)$, be distributed over an infinite one-dimensional areal x $(-\infty < x < +\infty)$. $F(N)$ is a continuous function, differentiable as much times as required, and $F(0) = F(K) = 0$, where K is the environmental carrying capacity. Moreover, $F'(0) = \alpha > 0$ and $F'(N) < \alpha$ for $0 < N \leqslant K$. If the specimens of this population randomly migrate over the areal and their radius of individual activity is ρ, then the dynamics of this spatially distributed population may be expressed by the equation ($D = \rho^2/4$)

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + F(N). \tag{8.88}$$

The classical result derived by A. N. Kolmogorov, I. G. Petrovsky and N. S. Piskunov in 1938 is that equation (8.88) has a solution of the running-wave type $N(x, t) = N(x + \lambda t)$, propagating from the right to the left at the velocity λ; as $t \to \infty$, $\lambda \to \tilde{\lambda} = 2\sqrt{\alpha D}$ and the wave form tends to the function $\tilde{N}(x)$ which is the solution

to

$$\tilde{\lambda}\frac{d\tilde{N}}{dx}=D\frac{d^2\tilde{N}}{dx^2}+F(\tilde{N}) \tag{8.89}$$

with boundary conditions $\tilde{N}(-\infty)=0$, $\tilde{N}(+\infty)=K$. It is proved that there is a convergence to this solution for a fairly broad class of initial distributions $N(x, 0)=N_0(x)$, provided that $0<N_0(x)\leqslant K$. For instance, $N_0(x)$ may be a finite function, that is a function which is nonzero on a certain finite segment of the x-axis and zero elsewhere. This initial distribution models a population explosion in a local domain of the areal. In the other case $N_0(x)$ may be a step-function of the form $N_0(x)=\{K,\ 0\leqslant x\leqslant\infty;\ 0,\ -\infty<x<0\}$. It is natural to call non-linear waves of this type *populational waves*. For instance, if the logistic law is chosen to govern the local population growth, i.e. $F(N)=\alpha N\left(1-\frac{N}{K}\right)$, then the asymptotic propagation velocity of the populational wave over the areal will equal $\tilde{\lambda}=2\sqrt{\alpha D}=\rho\sqrt{\alpha}$. Curiously enough, it does not depend upon the environmental carrying capacity K.

Naturally, a question arises: are the populational waves of this type found in real nature? The answer comes from the following experiment. A population of regular *Drosophila funebris* was released from a population box to a natural areal (a cesspit with rotting fruit and vegetables). By the trap-method the radius of individual activity for these flies was determined to be 14 m per one generation or 0.75 m a day. On the other hand, observations indicated that in 50 days the fly population on the local areal increased from 100 to 5000 specimens but showed no further growth. Estimating the Malthusian parameter α with the logistic model, we derived that $\alpha=0.16$ specimens a day. Hence $\tilde{\lambda}=0.3$ m a day. Observations showed that after reaching the population of 3000 specimens on the local areal, the flies began to spread beyond its limits. In about 55 days the appropriate population density was measured at 22 m from the border of the local areal. Consequently, we can conclude, that the real populational wave moved at an average velocity of $\tilde{\lambda}_{ex}\cong 0.4$ m a day. Allowing for the very low accuracy of measurements, we can say that almost a perfect agreement was obtained. Apparently, with sufficient reliability it may be said that in this experiment we were concerned with a populational wave of the Kolmogorov-Petrovsky-Piskunov type.

8.10. Non-linear waves in the resource-consumer system

Consider the following case. Suppose at a certain point in the areal filled by resource (ecologically active medium) there appears a population explosion of specimens—consumers of this resource. Consumers

randomly migrate over the areal, while the resource is stationary. As a result, a wave starts to propagate from the place of the explosion over the space covered by resource. Perhaps a most typical example of this phenomenon is the spread of the population of forest pests or the spread of the pest population over a cultivated field.

In the case of a one-dimensional unlimited areal x $(-\infty < x < +\infty)$ such a system (which will be termed resource-consumer system) may be characterized by equations of the form

$$\frac{\partial R}{\partial t} = F_R(R, N), \qquad \frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + F_N(R, N), \tag{8.90}$$

where $F_R = \alpha(R)R - V(R)N$, $F_N = kV(R)N - mN$.

Here $R(x, t)$ and $N(x, t)$ are the densities of the resource and the consumer, respectively, $V(R)$ is the trophic function, k is the efficiency of the resource processing, $\alpha(R)$ is the relative rate of the increment in resource, m is the natural mortality coefficient for the consumer, $D = \rho^2/4$, where ρ is the radius of the predator individual activity. It is readily seen that equations (8.90) represent a model of a spatially distributed predator-prey system with the fixed prey.

The original density distributions of the resource $[R_0(x)]$ and the consumer $[N_0(x)]$ provide initial conditions for (8.90): $R(x, 0) = R_0$, $N(x, 0) = N_0$.

Let $\alpha(R) \equiv 0$, i.e. the resource is only consumed without renewal. Introduce a new variable $u(x, t) = \int_0^t N\,dt$. Then the term-by-term integration of the second equation in (8.90) gives

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + k\int_0^t V(R)N\,dt - mu + N_0(x).$$

But from the first equation in (8.90) it follows that

$$R = R_0 - \int_0^t V(R)N\,dt.$$

From the same equation we can derive that

$$\varphi(R, R_0) = \int_{R_0}^{R} dR/V(R) = -\int_0^t N\,dt = -u,$$

hence, if we know the concrete form of the trophic function $V(R)$, we immediately find R as $R(u, R_0)$.

And eventually, instead of the system (8.90) we get one equation for u:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + \mathcal{F}(u, x),$$

$$\mathcal{F} = N_0(x) + kR_0(x) - kR(u, R_0) - mu. \tag{8.91}$$

Let $R_0(x) = \text{const}$. Besides, another important assumption will be made, that will be justified somewhat later. Modeling the population explosion we preassign $N_0(x)$ as a finitary function, which is zero for almost all x. Assume $N_0(x) \equiv 0$ in (8.91). Then

$$\mathcal{F} = \mathcal{F}(u) = k[R_0 - R(u, R_0)] - mu. \tag{8.92}$$

And $\mathcal{F}(0) = 0$ because $u = 0$ and $R = R_0$ when $t = 0$. Besides, there exists one more value $u_{\max} = \frac{k}{m}(R_1 - R_0)$, such that $\mathcal{F}(u_{\max}) = 0$.

$$\frac{d\varphi}{dR} = \frac{1}{V(R)} > 0$$

since $V(R) > 0$ for $R > 0$, and from monotonicity of $\varphi(R, R_0)$ it follows that the value $u_{\max}$ is unique. Calculating the derivative $\mathcal{F}'_u$ we obtain

$$\mathcal{F}'_u = -kR'_u(u, R_0) - m. \tag{8.93}$$

The derivative R'_u may be found as the derivative for the implicit function $\Phi(R, u) = \varphi(R, R_0) + u = 0$:

$$R'_u = -\frac{\partial\Phi/\partial u}{\partial\Phi/\partial R} = -\frac{1}{\partial\varphi/\partial R} = -V(R).$$

Then $\mathcal{F}'_u = kV(R) - m$ and $\mathcal{F}'(0) = kV(R_0) - m$. Since $V(R)$ steadily grows with R, and since the resource decreases with increasing population (and consequently with u), $\mathcal{F}'_u(u) < \mathcal{F}'_u(0)$ for $0 < u < u_{\max}$.

Thus we reduced the problem of the wave propagation in the resource-consumer system to the classical Kolmogorov-Petrovsky-Piskunov problem considered in the previous section. Consequently, there exists a unique stable solution of the form $u(x, t) = u(x + \lambda t)$, i.e. a wave, propagating over the areal at a velocity

$$\tilde{\lambda} = 2\sqrt{[kV(R_0) - m]D} = \varphi\sqrt{kV(R_0) - m}. \tag{8.94}$$

The wave form is specified by the expression $\tilde{N}(x) = d\tilde{u}(x)/dx$, where $\tilde{u}(x)$ is the solution to the problem

$$\tilde{\lambda}\frac{d\tilde{u}}{dx} = D\frac{d^2\tilde{u}}{dx^2} + \mathcal{F}(\tilde{u}), \tag{8.95}$$

$$\tilde{u}(-\infty) = 0, \qquad \tilde{u}(+\infty) = u_{\max}.$$

The condition for the initial resource density immediately follows from the expression for the wave velocity: $R_0 > R^*$, where R^* is the root of the equation $V(R^*) = m/k$. If $R_0 \leqslant R^*$, the wave fails to appear and the explosion remains localized, gradually damping out. As an illustration Fig. 53 presents several versions of

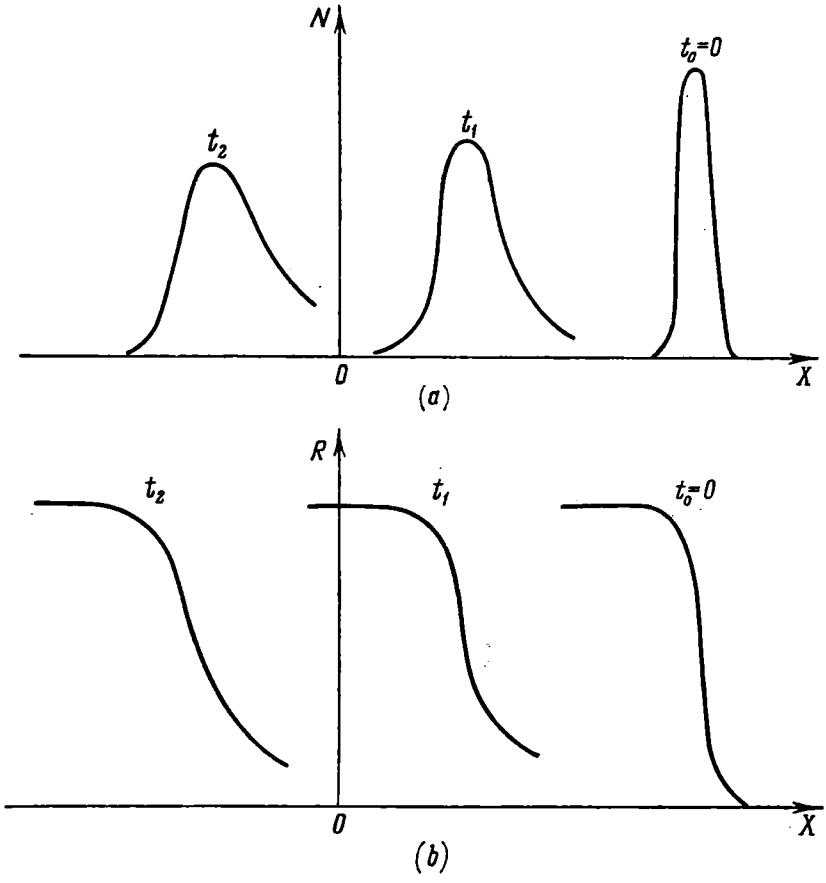

Fig. 53. Propagation of a solitary wave in the system "unrenewable resource-consumer", $t_0 < t_1 < t_2$. At the initial time $t_0 = 0$ there is a local outbreak of the consumer; (*a*) population wave for the consumer; (*b*) the wave of resource uptake.

the wave form for the population and the resource at successive points in time, obtained by a direct solution of equations (8.90) on a computer.

As an example consider the case when $V(R) = \gamma R$, i.e. a Volterra-type trophic function. Then $R = R_0 e^{-\gamma u}$ and $\mathcal{F}(u) = kR_0(1 - e^{-\gamma u}) - mu$. The wave propagation velocity is $\tilde{\lambda} = \rho\sqrt{k\gamma R_0 - m}$ and it increases with R_0, i.e. with the resource abundance, but this increase is even slower than linear.

Let us now estimate the validity of the above-accepted hypothesis, i.e. let us see how strong is the effect of the term $N_0(x)$, neglected

in (8.91), on the behavior of the propagating wave. Let $N_0(x) > 0$ for $x \in \Omega$ and $N_0(x) \equiv 0$ for $x \notin \Omega$. Suppose for definiteness that Ω is near the origin. Since the term $N_0(x)$ mostly affects the rear "tail" of the wave $u(x + \lambda t)$, it is sufficient to examine the behavior of the function $w(x, t) = u(x, t) - u_{\max}$. Then neglecting the terms of the order of $o(|w|)$, from (8.91) we get

$$\frac{\partial w}{\partial t} = D\frac{\partial^2 w}{\partial x^2} - bw + N_0(x),$$
$$b = -\mathcal{F}'_u(u_{\max}) \geqslant 0, \qquad D = \rho^2/4. \tag{8.96}$$

The solutions to equation (8.96) may be represented in the form

$$w(x, t) = e^{-bt}\int_\Omega \int_0^t \frac{N_0(\xi)}{\rho\sqrt{\pi\tau}} e^{-\frac{(x-\xi)^2}{\rho^2\tau}} d\tau\, d\xi. \tag{8.97}$$

Let $|x| \gg |\xi|$, i.e. consider $w(x, t)$ at those points, which the wave has already passed. Evaluating the integral in (8.97) by the Laplace method (as $(x/\rho)^2 \to \infty$), we get

$$w(x, t) \simeq ct^{3/2} e^{-bt} e^{-x^2/\rho^2 t}$$
$$c = (\rho\sqrt{\pi})^{-1}\int_\Omega N_0(\xi)\, d\xi. \tag{8.98}$$

Suppose now that the point of observation is moving at a rate $\tilde{\lambda} = \rho\sqrt{\mathcal{F}'_u(0)}$, so that $x/t = \tilde{\lambda}$. Substituting this relationship into (8.98), we will have

$$w(\tilde{\lambda}t, t) \simeq ct^{3/2} e^{-(\mathcal{F}'_u(0) - \mathcal{F}'_u(u_{\max}))} \tag{8.99}$$

or if we follow the x coordinate

$$w(x, x/\tilde{\lambda}) \simeq c(x/\tilde{\lambda})^{3/2} e^{-\delta x},$$
$$\delta = \frac{\tilde{\lambda}}{\rho} + \frac{b}{\tilde{\lambda}}. \tag{8.100}$$

Thus, the perturbation due to the neglected term $N_0(x)$, overtaking the wave, is exponentially small at the points sufficiently distant from the place of an explosion. Therefore, at significant distances from this place, i.e. from the domain where $N_0(x) \neq 0$, our hypothesis is well founded and the wave $u(x + \lambda t)$ represents a Kolmogorov-Petrovsky-Piskunov wave. Accordingly, the formulas (8.94) and (8.95) are valid for the asymptotic wave velocity and the form of the wave front in the system made up by the consumer and the unrenewable resource.

Let now $\alpha(x) \neq 0$, i.e. the resource is renewed after consumption. Unfortunately, in this case we failed to obtain any significant analyt-

ical result, such as for the unrenewable resource, for instance. However, direct computer experiments, i.e. the solution of (8.90) with a computer, gave rather interesting results. It turned out that under

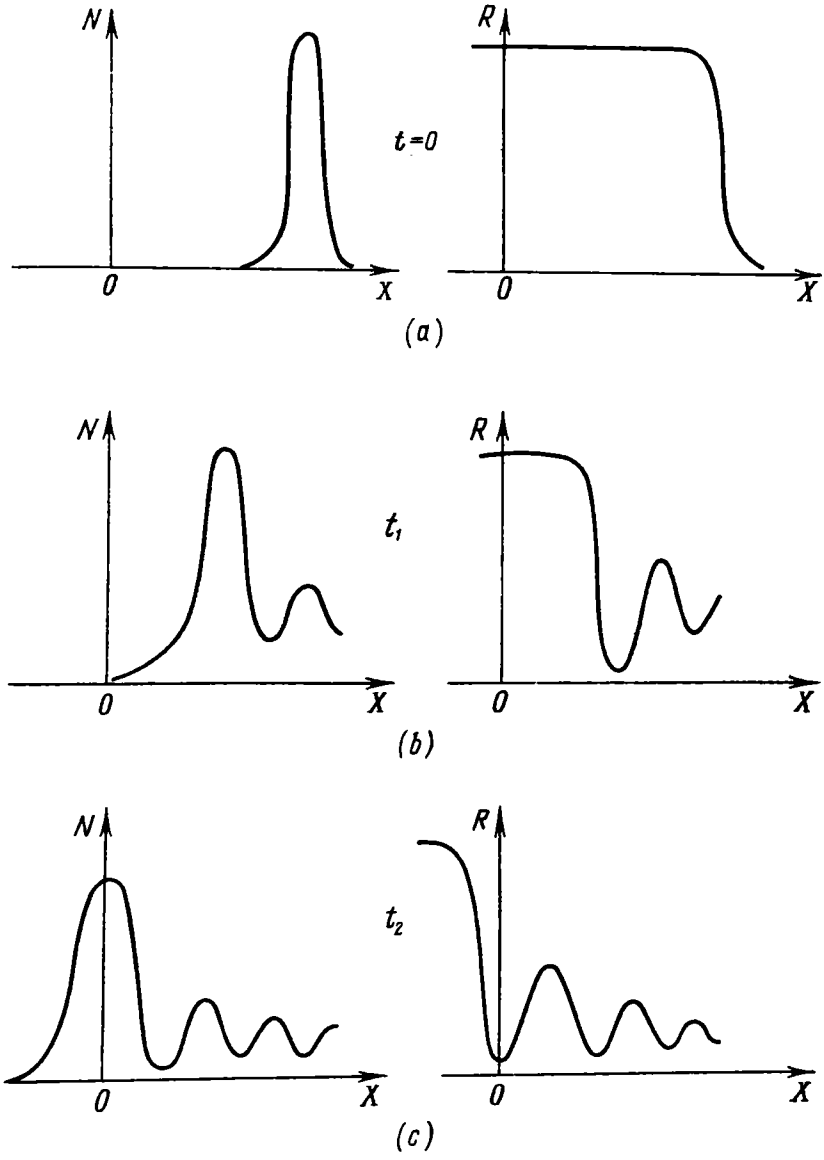

Fig. 54. Origination and propagation of a group of waves (wave train) in the system "renewable resource-consumer". (a)-(c) population waves (on the left) and waves of resource uptake (on the right) at successive points in time ($t_0 < t_1 < t_2$). At the initial point $t_0 = 0$ there is a local outbreak of the consumer population.

certain conditions a local population explosion generates not the only wave, but a whole wave succession, i.e. a number of waves following one another. The initial local perturbation (population ex-

plosion) in the ecologically active medium behaves as a peculiar generator of populational waves. For illustration, Fig. 54 displays results of a computer run, which demonstrates the formation of a wave succession in the environment with a renewable resource.

8.11. Conclusion

Though in nature we find a wide variety of very different regulation mechanisms related to spatial distribution of organisms, and ecologists think that generally there are no spatially homogeneous communities, only a few models of this type have been developed in mathematical ecology. Apparently this may be explained by the sharp increase in purely mathematical difficulties. A similar case developed, for instance, in continuous medium mechanics, where in spite of the long history of this science investigation of the problems of hydrodynamic stability (incidentally, very similar to our problems) began quite recently.

8.12. Notes and bibliography

To 8.1. Inhomogeneity of biomass distribution in depth is most pronounced in ecosystems of tropical oceanic regions, see, for instance,

Functioning of pelagic communities in tropical oceanic regions, Nauka, Moscow, 1971 (in Russian).

The radius of individual activity is determined referring to *Drosophila* in the paper:

Timofeev-Resovsky N. V., Svirezhev Yu. M., "On the opposite effects of selection on the genotype and the trait for a mutation linked with sex," Nauka, Moscow, 1967, pp. 155-170. (*Problems of Cybernetics*, Vol. 18) (in Russian).

For the trigger mechanisms of species formation, related to spatial isolation, see:

Timofeev-Resovsky N. V., Vorontsov N. N., Yablokov A. V., *A short essay on evolution theory*, Nauka, Moscow, 1969, pp. 158-172 (in Russian).

To 8.2. The most complete study of the problem of stationary phytoplankton distributions in a physically inhomogeneous environment allowing for uptake by zooplankton is presented in the work:

Krapivin V. F., *Mathematical determinate ecosystem models*, Inst. of Radio-Electronics Acad. Sci. USSR, Moscow, 1972 (Preprint No. 82) (in Russian).

To 8.3. Effect of migration on stability of biological populations and communities was discussed in a series of experimental works:

Huffaker C. B., "Experimental studies on predation: dispersion factors and predator-prey oscillations," *Hilgardia*, 27, 14, pp. 343-383, 1958;
Huffaker C. B., Shea K. P., Herman S. G., "Experimental studies on predation: complex dispersion and levels of food in an acarine predator-prey interaction," *Hilgardia*, 34, 9, pp. 305-329, 1963;
Sakai K., Narise T., Hiraizumi Y., Iyama S., "Studies on competition in plants and animals. IX. Experimental studies on migration in *Drosophila melanogaster*," *Evolution*, 12, 1, pp. 93-101, 1958;

Southwood T. R. E., "Migration of terrestrial arthropods in relation to habitat," *Biol. Rev.*, 37, 1, pp. 171-214, 1962;

and in theoretical surveys:

Hatchinson G. E., "Homage to Santa Rosalia, or why are there so many kinds of animals?," *Amer. Natur.*, 93, 870, pp. 145-159, 1959;

Levin S. A., "Population dynamics in heterogeneous environments," *Ann. Rev. Ecol. Systematics*, 7, pp. 287-310, 1976.

The results of the present section are presented in the paper:

Logofet D. O., "Can migration stabilize the ecosystem? (Mathematical aspect)," *Zhur. Obsh. Biol.*, 39, 1, pp. 123-128, 1978 (in Russian).

It should be noted that in the works:

Hilborn R., "The effect of spatial heterogeneity on the persistence of predator-prey interaction," *Theor. Pop. Biol.*, 8, 3, pp. 346-355, 1975,

where random migration, equiprobable with respect to direction, is modeled, and

Allen G. C., "Mathematical models of species interactions in time and space," *Amer. Natur.*, 109, 967, pp. 319-342, 1975,

where biological interactions were specified by difference equations, and the migration process between adjacent subsystems was symmetric, a similar conclusion about inability of such migration to stabilize the biocommunity is derived. Notice that among the two principle schemes considered in the second work: (1) migration takes place after the act of biological interaction, and (2) migration precedes it—only the first one may be regarded as the discrete analogy of the systems considered in this section.

There may be other approaches to the mathematical study of migration stabilizing effects. For instance, in the work

Hastings A., "Spatial heterogeneity and the stability of predator-prey systems," *Theor. Pop. Biol.*, 12, 1, pp. 37-48, 1977,

the model is concerned not with populations within habitats, but with the fraction (of the total amount) of those habitats, which contain specimens of the predator and the prey. As within every habitat communities are thought to die out in a finite time-period, stability of a non-trivial equilibrium in such a model implies that migration sustains the regional existence of the community.

An analysis of such a migration using the methods of simulation modeling is given in Chapter 6 of the book:

Maynard Smith J., *Models in ecology*, Cambridge Univ. Press, Cambridge, 1974.

To 8.4. Systems with migration patterns, more complex than in this section, are usually studied by methods of simulation modeling. For instance, dynamics of two predator-prey pairs linked together by migration (a system similar to (8.37), but with different versions of non-linear relationships between migration and species populations) was studied by computer methods in the work:

Jones D. D., "Stability implications of dispersal linked ecological models," Publications of IIASA, RM-75-44, Laxenburg, 1975,

where a considerable number of phase portraits in the plane is presented (the populations of the prey and the predator average for two habitats). Model results for the Volterra predator-prey pairs with self-limitation among the prey, linked by migration, which occurs only in certain phases of the cyclic dynamics in subsystems, are discussed in the paper:

Zeigler B. P., "Persistence and patchiness of predator-prey systems induced by discrete event population exchange mechanisms," *J. Theor. Biol.*, 67, 4, pp. 687-713, 1977.

To 8.5. The line of reasoning of this section generalizes for the case of arbitrary interactions within the subsystem the small parameter method, developed for n predator-prey pairs in the work:

Chewning W. C., "Migratory effects in predator-prey models," *Math. Biosci.*, 23, 3/4, pp. 253-262, 1975,

where the migration pattern (8.20) (without the assumption about ε being small) is also analysed. In the work:

Freedman H. I., Waltman P., "Mathematical models of population interaction with dispersal. I. Stability of two habitats with and without a predator," *SIAM J. Appl. Math.*, 32, 3, pp. 631-648, 1977,

where a detailed investigation of the general model for two interacting populations linked by migration is performed, in particular, it is proved that the equilibrium $x^*(\varepsilon)$ exists not only in the regular case (i.e. when the Jacobian (8.49) is nonzero), but also in some singular cases, and the sufficient conditions are derived for stability.

To 8.6. Description of the genetic drift processes in spatially distributed populations in terms of diffusion equations has long been used (since the 1930's) in mathematical genetics. In mathematical ecology the application of diffusion equations to account for dynamics of spatially distributed communities started with the work:

Skellam J. G., "Random dispersal in theoretical population," *Biometrika*, 38, 2, pp. 196-218, 1951.

The diffusive instability concept first appeared in works on hydrodynamics, concerned with the study of stability for some established flows of viscous liquid (cf.

Lin C. C., *The Theory of Hydrodynamic Stability*, Cambridge University Press, Cambridge, 1955).

Presenting this concept as applied to spatially distributed communities, we basically follow the paper:

Segel L. A., Jackson J. L., "Dissipative structure: an explanation and an ecological example," *J. Theor. Biol.*, 37, 3, pp. 545-559, 1972.

To 8.7 and 8.8. Numerous problems concerned with applications of nonlinear diffusion equations in ecology may be found in the book:

Fife P. C., *Mathematical Aspects of Reacting and Diffusing Systems*, Springer-Verlag, Berlin, 1979.

Representing the material of Section 8.8 we used the works:

Razževaikin V. N., "On the origination of dissipative structures in a system of two reaction-diffusion equations," *Dokl. Acad. Nauk*, 22, 3, pp. 839-841, 1980;

Razževaikin V. N., "On the origination of stationary dissipative structures in a predator-prey type system," In: "*Self-oscillating wave processes in systems with diffusion*," Gorky State Univ. Press, Gorky, pp. 243-248, 1981 (In Russian),

where one may find a complete mathematical treatment of the problems of origination of spatial structures in a system of two non-linear diffusion equations. Obviously, all the models of spatially distributed predator-prey type systems fall into this class.

To 8.9. The classical work:

Kolmogorov A. N., Petrovsky I. G., Piskunov N. S., "The study of diffusion equations, related to the increase in the amount of substance, and their application to one biological problem,"

was published in 1938 in the *Moscow State Univ. Bulletin. Series A. Mathematics and mechanics.* Vol. 1, pp. 1-26 (in Russian).

It is interesting that similar problems appear in the combustion theory, and there is a large body of literature on that subject. In the recently published book:

Zeldovich Ya. B., Barenblatt G. I., Librovich V. B., Makhviladze G. M., *Mathematical combustion and explosion theory*, Nauka, Moscow, 1980 (in Russian),

there is a detailed survey of literature.

Experimental data on the propagation of a populational wave of *Drosophila* flies is taken from the above-cited paper by N. V. Timofeev-Resovsky and

Yu. M. Svirezhev (see bibliography for Section 8.1).

Among the recent works on populational waves the paper:

Kennedy C. R., Aris R., "Traveling waves in a simple population model involving growth and death," *Bull. Math. Biol.*, 42, 3, pp. 397-430, 1980,

should be mentioned, where a survey of the problem may be found.

To 8.10. The problem of the wave propagation in the system "non-renewable resource-consumer" found its complete solution (through reduction to the classical problem of Kolmogorov-Petrovsky-Piskunov and evaluation of effect of the neglected term $N_0(x)$) in the paper:

Gigauri A. A., Svirezhev Yu. M., "Wave propagation in the resource-consumer system," *Dokl. Acad. Nauk SSSR*, 258, 5, pp. 1274-1276, 1981 (in Russian).

To 8.11. The problem of origination of stable spatial structures in ecological systems is very closely related to the general existence problem of dissipative structures in physical, chemical and biological systems. These fundamentally unstable structures owe their existence to the continuous energy flow through the system. And while in mechanics examples of such structures have long been known (gyroscopes), their prevalence in biology (morphogenesis) started to be mentioned, perhaps only with the works of I. Prigogine. In the works of Prigogine, Nicolis, et al., the analytical methods for this kind of problem were worked out (on the "physical" level of rigour). Numerous works of this school of thought are summerized and systematized in the book:

Nicolis G., Prigogine I., *Self-Organization in Non-Equilibrium Systems*, Wiley, N.Y.-London, 1977.

Concerning the dissipative structures in ecology, there is a good survey:

Levin S. A., "Spatial Patterning and Structure of Ecological Communities," In: *Some mathematical questions in biology*, VII, AMS Publ., Providence, Rhode Island, 1976.

And finally we recommend the book:

Okubo A., *Diffusion and ecological problems. Mathematical models*, Springer-Verlag, Berlin, 1980,

which is rich in experimental data and closely related to purely ecological problems.

CHAPTER 9

STABILITY AND COMPLEXITY IN ECOSYSTEM MODELS

9.1. Ecological introduction

Among ecologists it is taken almost as an axiom that communities which are more complex in structure are more stable. There is a wide variety of arguments in favor of this thesis, supported by observations in real ecosystems. Thus, for instance, laboratory systems of only two species, the predator and the prey, most usually prove to be unstable; population explosions of pests are more typical of agrocenosis than of natural ecosystems, and their effect is more disastrous when the crops are monocultures. By contrast, the communities of rain forests, rich in specific composition and interspecific connections, demonstrate very stable functioning: there are no population explosions, population oscillations are much less pronounced than in forests of the subarctic zone with less species diversity and relatively greater populations. It is believed that ecosystems of complex structures are more stable under perturbations of environmental factors and the random oscillations in populations of some of the species, whereas more simple structures, such as the subarctic fauna communities, e.g. subject to sharp population oscillations, are unable to dampen out the perturbating effects.

But practically each of these arguments and observations may also find another interpretation, with no appeal to ecosystem complexity. Thus, the greater stability of natural ecosystems as against agrocenoses may be attributed to the longer coevolution period of species making up natural ecosystems, and the greater stability of trophic communities as compared with communities of the subarctic zone may be explained by destabilizing effects of sharp oscillations in climatic conditions.

We may remark that all these speculations are based not on strict definitions of the notions of ecosystem complexity and of the complexity measure, but rest only on the intuitive ideas that an increase in such ecosystem parameters as the number of species and trophic levels, the number of interspecific connections and their strength (or intensity) comply with higher structural complexity. And though we have no formal definition for ecosystem complexity, which would be similar in universality, say, to the definition of stability via

equilibrium stability in an appropriate model, still the mentioned ecosystem parameters are explicitly present in systems of model equations, thus enabling one to judge about the influence of these parameters on model stability. The problem is thereby transmitted to the field of mathematical models of ecosystem dynamics, where the analysis of the relation between stability and complexity is usually referred to as *complexity versus stability*.

The present chapter is concerned with some approaches to the complexity-versus-stability problem, and as it will be shown below, the mathematical analysis of the problem so far gives no preference to any of the two opposite ecological viewpoints.

9.2. Stability of systems without self-regulation

We shall begin the analysis of community models in respect of the relation between stability and complexity with the investigation of a community of two trophic levels with n species in each. If there is no self-regulation and competition among species in one and the same level, then the community dynamics in the class of Volterra equations is modeled by the system

$$\begin{aligned} \frac{dH_i}{dt} &= H_i\left(b_i - \sum_{j=1}^{n} \beta_{ij}P_j\right), \qquad i = 1, \ldots, n, \\ \frac{dP_i}{dt} &= P_i\left(-g_i + \sum_{j=1}^{n} \gamma_{ij}H_j\right). \end{aligned} \tag{9.1}$$

Here $H_i(t)$ and $P_i(t)$ are the populations of the ith prey and predator species, respectively, b_i, g_i, β_{ij}, γ_{ij} are positive parameters. We impose no more restrictions on the pattern of trophic links between the two levels—each predator-species may arbitrarily specialize in the uptake of prey-species. The only natural requirement for the combination of model parameters is that there exists a positive equilibrium $[\mathbf{H}^*, \mathbf{P}^*]$, defined as the positive solution to the partitioned system of equations

$$\Gamma\mathbf{H}^* = \mathbf{g}, \qquad \mathrm{B}\mathbf{P}^* = \mathbf{b} \tag{9.2}$$

with non-negative $n \times n$-matrices $\Gamma = \| \gamma_{ij} \|$ and $\mathrm{B} = \| \beta_{ij} \|$ and the right-hand side vectors $\mathbf{g} = [g_i, \ldots, g_n]^T$ and $\mathbf{b} = [b_1, \ldots, b_n]^T$.

Linearization of (9.1) at the equilibrium point $[\mathbf{H}^*, \mathbf{P}^*]$ yields the community matrix, built of four $n \times n$ blocks:

$$A = \begin{Vmatrix} 0 & -\mathrm{B}^* \\ \Gamma^* & 0 \end{Vmatrix}, \tag{9.3}$$

where B* and Γ* are matrices with elements

$$\beta^*_{ij} = H^*_i \beta_{ij}, \qquad \gamma^*_{ij} = P^*_i \gamma_{ij}. \tag{9.3'}$$

It may be shown that the characteristic polynomial $D_{2n}(\lambda)$ for matrix A of the form (9.3) is represented by a polynomial of degree n in λ^2. In fact, we expand the characteristic polynomial

$$D_{2n}(\lambda) = \begin{vmatrix} \lambda I & B^* \\ -\Gamma^* & \lambda I \end{vmatrix} \tag{9.4}$$

in the first n rows. The first term in our sum is clearly

$$\det \lambda I \cdot \det \lambda I = \lambda^{2n}.$$

Consider next the minor made up of columns with numbers $i_1, \ldots, i_n$ and suppose the i_1th, ..., i_sth of them belong to the submatrix λI while the i_{s+1}th, ..., i_nth columns are from the submatrix B* (s may take on the values $(n-1)$, $(n-2)$, ..., 1). After an appropriate rearrangement in its rows this minor (up to a sign) will have the form

$$\det \begin{pmatrix} 1 & 2 & \ldots & n \\ i_1 & i_2 & \ldots & i_n \end{pmatrix} = \pm \left| \begin{array}{cccc|c} \lambda & & & & \\ & \lambda & & & B^{*\prime}_s \\ & & \ddots & & \\ & & & \lambda & \\ \hline 0_{(n-s)\times s} & & & & B^{*\prime\prime}_s \end{array} \right| = \pm \lambda^s \det B^{*\prime\prime}_s, \tag{9.5}$$

where $B^{*\prime}_s$ and $B^{*\prime\prime}_s$ are some submatrices of B*. The cofactor for this minor is constructed from the n lower rows of A, $(n-s)$ columns of the submatrix $(-\Gamma^*)$ and the s columns of the submatrix λI. In consequence, similarly to (9.5) we derive that this cofactor equals

$$\pm \det A \begin{pmatrix} n+1 & n+2 & \ldots & 2n \\ j_1 & j_1 & \ldots & j_n \end{pmatrix} = \pm \lambda^s \det(-\Gamma^{*\prime}_s), \tag{9.6}$$

where $\Gamma^{*\prime}$ is the appropriate submatrix of Γ^*.

From (9.5) and (9.6) it follows that all the terms in the expansion of the characteristic determinant (9.4) have the form

$$\pm \lambda^{2s} \det B^{*\prime\prime}_s \cdot \det \Gamma^{*\prime}_s,$$

i.e. the characteristic polynomial $D_{2n}(\lambda)$ contains only even powers of λ:

$$D_{2n}(\lambda) = \lambda^{2n} + a_2\lambda^{2n-2} + \ldots + a_{2n-2}\lambda^2 + a_{2n}. \tag{9.7}$$

Consequently, if the number $\lambda = \zeta + i\xi$ occurs in the spectrum of the community matrix A, then $-\lambda = -\zeta - i\xi$ is also an eigenvalue of A. So, either the spectrum of A is entirely composed of pure imaginary numbers, in which case the equilibrium [H*, P*]

is neutrally stable, or at least one eigenvalue in the spectrum has a positive real part, and the equilibrium is unstable.

Thus the n-predator-n-prey system (9.1) at best has the same stability properties as the corresponding one-predator-one-prey system (Section 3.2), and in general it is more likely that among the $2n$ roots of the polynomial (9.7) some will not be pure imaginary, i.e. the equilibrium will be unstable. In particular instances of systems (9.1) we can easily see that both cases are possible, i.e. both neutral stability of the equilibrium with the trajectory oscillating about it, and instability with some species declining to extinction.

Notice that this conclusion is naturally extended to include systems of a more general form than (9.1), namely systems of m interacting species with their populations $N_i(t)$ governed by the equations

$$\frac{dN_i}{dt} = F_i(N_i)\, G_i(\mathbf{N}), \qquad i = 1, \ldots, m, \tag{9.8}$$

where the function $G_i(\mathbf{N})$ is independent of N_i, that is,

$$\partial G_i(\mathbf{N})/N_i \equiv 0, \qquad i = 1, \ldots, m. \tag{9.9}$$

The equations (9.8) imply that the intrinsic growth rate $F_i(N_i)$ is factored out from the total sum of interactions with the other species. If the non-trivial equilibrium $\mathbf{N}^*$ is determined as the positive solution to the equations $G_i(\mathbf{N}^*) = 0$ $(i = 1, \ldots, m)$, then all the diagonal elements of the community matrix are zero:

$$a_{ii} = \partial F_i(N_i^*)/\partial N_i \cdot G_i(\mathbf{N}^*) = 0, \qquad i = 1, \ldots, m,$$

i.e. the community is entirely composed of species which have neither self-limitation nor self-stimulation at equilibrium. Since the sum of eigenvalues of A is zero:

$$\lambda_1 + \ldots + \lambda_m = a_{11} + \ldots + a_{mm} = 0,$$

again only two alternatives are possible—either all λ_j are pure imaginary (pairwise complex conjugate), or there are λ_j with negative as well as with positive $\operatorname{Re} \lambda_j$. The first alternative is realized in systems with $m = 2$ species, when $m > 2$ the second one is more probable.

Thus, in the considered, rather broad, class of simple models the stability may only impair with the number of species. It is intuitively clear that all the other things being equal, the system with a greater number of species should be considered more complex, therefore here we have an example of how an increase in complexity of the community model impairs its stability.

9.3. Effect of predators on stability in competitive community

In the preceding section we have looked at the relation between stability and increase in the number of species in a two-trophic-level community. And how will the stability be affected by the increase in the number of trophic levels themselves? Is the stability of, say, a one-level system improved by the addition of the second level (the predators, preying on the species in the first level)? The literature abounds in examples which give controversial answers to this question. In some works it was found that stability in one trophic level may be accompanied by instability of a two-level community (I), in others—that an unstable competitive prey community may be stabilized by the effect of a predator, the two-level system being stable as a result (II). Besides, arguments were adduced in favor of the fact that stability in one level should provide stability to the second level through feed-back mechanisms, and hence make the whole community stable (III); and vice versa, instability in one level should bring instability to the system as a whole (IV). The conclusion which sums up this discussion is that it seems we are not to expect a general answer to all these questions, which would be independent of the specific features of trophic patterns under consideration.

The simplest model which can demonstrate all the above phenomena is the Volterra one-predator-one-prey system with competition in the prey level. In notations of the preceding section the model equations take the form

$$\begin{aligned} dH_1/dt &= H_1\,(b_1 - \alpha_{11}H_1 - \alpha_{12}H_2 - \beta_1 P),\\ dH_2/dt &= H_2\,(b_2 - \alpha_{21}H_1 - \alpha_{22}H_2 - \beta_2 P),\\ dP/dt &= P\,(-g + \gamma_1 H_1 + \gamma_2 H_2), \end{aligned} \tag{9.10}$$

where $\alpha_{ij} \geqslant 0$ are the competition coefficients for prey-species.

Suppose (9.10) has a non-trivial equilibrium $[H_1^*, H_2^*, P^*]$ and a partially positive one $[H_1^\circ, H_2^\circ, 0]$, and to begin with consider the prey dynamics in the absence of the predator $[P(t) \equiv 0]$. Then for the equilibrium $\mathbf{H}^\circ$ to be stable in its linear approximation it is necessary and sufficient that the condition

$$\det \|\alpha_{ij}'\| = \alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0, \tag{9.11}$$

be satisfied, which implies that the competition effect between specimens of one and the same species is stronger than between those of different species.

We turn now to stability conditions for the non-trivial equilibrium $[H_1^*, H_2^*, P^*]$ in the full system. Linearization of (9.10) yields the

3×3 community matrix

$$A = \begin{Vmatrix} -A^* & -B^* \\ \gamma^* & 0 \end{Vmatrix}, \tag{9.12}$$

where the 2×2 block B^* is defined in (9.3′) and likewise

$A^* = \operatorname{diag}\{H_1^*, H_2^*\} \| \alpha_{ij} \|$ and $\gamma^* = [\gamma_1 P^*, \gamma_2 P^*]$.

To compare the stability conditions for one level with those of the whole system, look at a more particular case, where

$$\beta_1^* = \beta_2^* = \beta, \qquad \gamma_1^* = \gamma_2^* = \gamma. \tag{9.13}$$

In particular this may be the case when $H_1^* = H_2^*$ and the preys of both species are consumed with the same intensity, i.e. $\beta_1 = \beta_2$ and they are equally "useful" for the predator, i.e. $\gamma_1 = \gamma_2$. Then the characteristic polynomial for the matrix (9.12) is

$$D_3(\lambda) = \lambda^3 + (\alpha_{11} + \alpha_{22})\lambda^2 + (\det \| \alpha_{ij} \| + 2\beta\gamma)\lambda + \beta\gamma(\alpha_{11} + \alpha_{22} - \alpha_{12} - \alpha_{21}), \tag{9.14}$$

and the Hurwitz determinants are

$$\Delta_1 = \alpha_{11} + \alpha_{22} > 0,$$
$$\Delta_2 = (\alpha_{11} + \alpha_{22}) \det \| \alpha_{ij} \| + \beta\gamma(\alpha_{11} + \alpha_{22} - \alpha_{12} - \alpha_{21}),$$
$$\Delta_3 = \beta\gamma(\alpha_{11} + \alpha_{22} - \alpha_{12} - \alpha_{21})\Delta_2.$$

If $\Delta_2 > 0$, the condition $\Delta_3 > 0$ is equivalent to

$$\alpha_{11} + \alpha_{22} - \alpha_{12} - \alpha_{21} > 0, \tag{9.15}$$

and it may be given an interpretation analogous to (9.11) in that intraspecific prey competition is stronger than the interspecific one.

Since the stability criteria for matrix (9.12) are the conditions (9.15) and $\Delta_2 > 0$, it is clear that for stability it is sufficient that, say, (9.15) and (9.11) are satisfied—in so doing both the isolated prey level and the system as a whole are stable (case III). Yet, if β and γ are big enough, i.e. the preying process affects the community dynamics to a greater degree than competition, then the condition $\Delta_2 > 0$ may hold even when (9.11) is not satisfied, thus making for stabilization of unstable competition (case II). On the other hand, the competition coefficient may be chosen, such that the condition (9.11) is met, while (9.15) is not, i.e. the preying effect will destabilize the stable competitive community (case I). Lastly, the conditions opposite to (9.11) and (9.15) make for instability within both a trophic level and the whole system (case IV). The graphic illustration of the occurrence of all these cases in the space of competition coefficients is given in Fig. 55.

Thus already within the framework of one and the same qualitative community structure there may be any variant of the relation between single level stability and two-level system stability, accord-

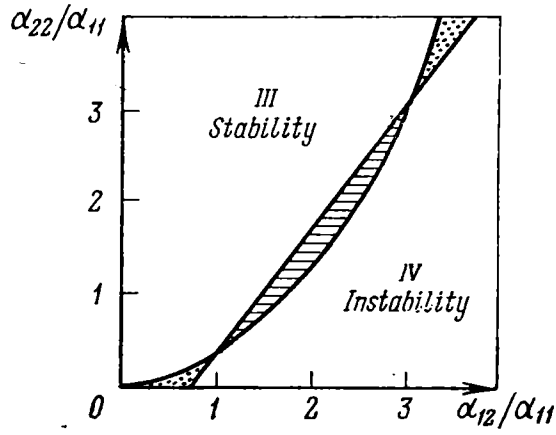

Fig. 55. Intersection of domains of stability and instability, given by conditions (9.11) and (9.15) in the space of parameters (α_{12}/α_{11}, α_{21}/α_{11}, α_{22}/α_{11}). To make it more vivid the typical 2-dimensional cross-section by the plane $\alpha_{12} = 3\alpha_{21}$ is presented. Roman numerals indicate domains, which belong to the cases described in the text (*I*—horizontal shading, *II*—point shading).

ing to particular quantitative values of the interaction parameters. Thereby a change to more complex trophic structure in this case may have a wide variety of effects on system stability.

9.4. Stability of n predator-prey pairs linked by competition

The present section is concerned with the community of two trophic levels, their interaction being described by the system (9.1). If each prey species is taken up only by one of the n predator species (the highly specialized predator), then the community actually splits into n separate predator-prey pairs. As we know (cf. Chapter 3), these pairs have a non-trivial neutrally stable equilibrium and periodic trajectories in the neighborhood of this equilibrium.

We complicate the system a bit assuming that the preys of the adjacent pairs compete for some resource (Fig. 56), and suppose that competition affects system dynamics much less than the trophic interactions. Then with the introduction of the small parameter $\varepsilon > 0$ the system of Volterra equations may be written in the form (for notational convenience we assume $H_0(t) \equiv H_{n+1}(t) \equiv 0$)

$$\begin{aligned} \frac{dH_i}{dt} &= H_i\,[b_i - \varepsilon\,(H_{i-1} + H_{i+1}) - \beta_i P_i], \\ \frac{dP_i}{dt} &= P_i\,[-g_i + \gamma_i H_i], \qquad i = 1, \ldots, n. \end{aligned} \tag{9.16}$$

The system (9.16) has an equilibrium with the components

$$H_i^* = g_i/\gamma_i, \qquad i = 1, \ldots, n,$$
$$P_i^* = [b_i - \varepsilon (H_{i-1}^* + H_{i+1}^*)]/\beta_i, \tag{9.17}$$

which are positive if

$$\varepsilon < \min_i \{b_i/(H_{i-1}^* + H_{i+1}^*)\}, \tag{9.18}$$

i.e. in any case for an ε small enough. Thus, the weak connection via competition maintains the non-trivial equilibrium in the system,

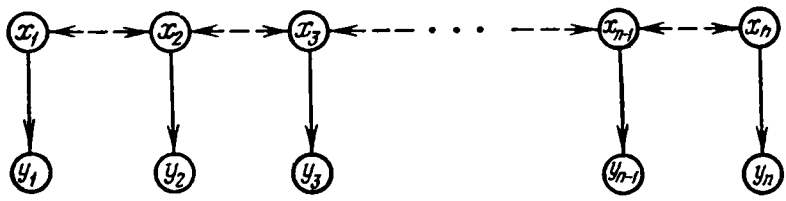

Fig. 56. Combination of n predator-prey pairs connected by competition among the preys; full arrows belong to predation relations, broken arrows present relations of competition.

though the predator equilibrium population is reduced as compared with the case of pairs in isolation.

To examine the effect of the system complication of this kind upon equilibrium stability study the eigenvalues $\lambda_k(\varepsilon)$ of the matrix in system (9.16), linearized at equilibrium (9.17). The explicit form of the relationship between ε and the equilibrium populations enables us to estimate $\lambda_k(\varepsilon)$ in a more simple way, without resorting to the method developed in Section 8.5.

The community matrix in the Volterra system (9.16) has the form (cf. Section 4.5)

$$\mathcal{A}(\varepsilon) = -\operatorname{diag}\{H_1^*, \ldots, H_n^*, P_1^*, \ldots, P_n^*\} \times$$
$$\times \left\| \begin{array}{c|c} A(\varepsilon) & \operatorname{diag}\{\beta_1, \ldots, \beta_n\} \\ \hline \operatorname{diag}\{-\gamma_1, \ldots, -\gamma_n\} & 0 \end{array} \right\|, \tag{9.19}$$

where the competition pattern is specified by the matrix

$$A(\varepsilon) = \left\| \begin{array}{cccccc} 0 & \varepsilon & & & & \\ \varepsilon & 0 & \varepsilon & & & \\ \cdot & \cdot & \cdot & \cdot & & \\ & \cdot & \cdot & \cdot & \cdot & \\ & & & \cdot & \varepsilon & 0 & \varepsilon \\ & & & & & \varepsilon & 0 \end{array} \right\|. \tag{9.20}$$

Expanding the characteristic determinant for matrix (9.19)

$$D_{2n}(\lambda) = \det(\lambda I - \mathcal{A}(\varepsilon))$$

in elements of the last row, and then expanding the resulting minors, the first one in elements of the nth column, the second—in those of the $(2n-1)$th column, we get:

$$D_{2n}(\lambda) = (\lambda^2 + \beta_n \gamma_n H_n^* P_n^*) D_{2(n-1)}(\lambda) - \varepsilon^2 H_n^* H_{n-1}^* \lambda^2 D_{2(n-2)}(\lambda), \quad (9.21)$$

and direct calculations yield

$$D_0(\lambda) \equiv 1, \qquad D_2(\lambda) = \lambda^2 + \beta_1 \gamma_1 H_1^* P_1^*. \quad (9.22)$$

In consequence, we see that $D_{2n}(\lambda)$ is a polynomial of order n in λ^2, i.e. as in the preceding section, either both values with negative and with positive real parts occur in the spectrum of $\mathcal{A}(\varepsilon)$ and the equilibrium is unstable, or all the eigenvalues are pure imaginary and the equilibrium is neutrally stable. Accordingly, we may already state that the complication considered—the combining into the competitive pattern (9.20)—fails to stabilize the system. Whether it will preserve the neutral character of equilibrium in the isolated pairs or destabilize it, will be evident from the estimate of $\lambda_k(\varepsilon)$.

To obtain an estimate of $\lambda_k(\varepsilon)$ with an accuracy of $O(\varepsilon^2)$ we may neglect the second summand in (9.21), because it contains terms of order ε^2 and higher. Then with account of (9.22) we get

$$D_{2n}(\lambda) \approx (\lambda^2 + \beta_n \gamma_n H_n^* P_n^*)(\lambda^2 + \beta_{n-1} \gamma_{n-1} H_{n-1}^* P_{n-1}^*) \ldots (\lambda^2 + \beta_1 \gamma_1 H_1^* P_1^*),$$

whence we see that pure imaginary roots are

$$\lambda_k^{\pm}(\varepsilon) = \pm i \sqrt{g_k [b_k - \varepsilon (H_{k-1}^* + H_{k+1}^*)]}, \qquad k = 1, \ldots, n, \quad (9.23)$$

with an accuracy of $O(\varepsilon^2)$. Thus, for sufficiently small ε the equilibrium keeps its neutral stability, and if we recall that the frequency of oscillations about equilibrium for a pair in isolation is $\sqrt{b_k g_k}$, it becomes apparent from (9.23) that a weak competition in the prey level results in a decrease in the frequency of oscillations within the linear approximation of trajectories.

On the other hand, one may easily see that the growing ε brings about violation of conditions necessary for the roots of $D_{2n}(\lambda)$ to be pure imaginary, i.e. eigenvalues with $\operatorname{Re} \lambda(\varepsilon) > 0$ appear and the equilibrium becomes unstable. Therefore the strengthening of competition links among pairs destabilizes the community.

If the presence of interspecific competition is assumed in the predator level, instead of the prey-level, and the competition is not for the prey-species, but for some non-exterminable resources (say, the habitat), then the system dynamics will be governed by the

equations

$$\frac{dH_i}{dt} = H_i\,[b_i - \beta_i P_i], \qquad i = 1, \ldots, n,$$
$$\frac{dP_i}{dt} = P_i\,[-g_i + \gamma_i H_i - \varepsilon\,(P_{i-1} + P_{i+1})]. \tag{9.24}$$

In much the same way we can study the stability of the non-trivial equilibrium in system (9.24)

$$H_i^* = [g_i + \varepsilon\,(P_{i-1}^* + P_{i+1}^*)]/\gamma_i, \qquad P_i^* = b_i/\beta_i, \tag{9.25}$$

which this time obviously exists for any $\varepsilon > 0$. The analog of the relationship (9.21) for the characteristic polynomial is

$$D_{2n}(\lambda) = (\lambda^2 + \beta_n \gamma_n H_n^* P_n^*)\, D_{2(n-1)}(\lambda) - \varepsilon^2 P_n^* P_{n-1}^* \lambda^2 D_{2(n-2)}(\lambda),$$

whence the estimate for the eigenvalues is

$$\lambda_k^{\pm}(\varepsilon) = \pm\, i \sqrt{b_k\,[g_k + \varepsilon\,(P_{k-1}^* + P_{k+1}^*)]}. \tag{9.26}$$

Thus, the influence of interspecific competition among the predators is similar to the above with the sole difference that the frequencies of oscillations about the neutrally stable equilibrium in the linear approximation are accordingly increasing.

9.5. Stability of randomly structured communities

In the previous sections, the problem of complexity versus stability was investigated for models of two-level systems, with the complexity increasing by variations in only one of the system properties: increase in the number of species (Section 9.2), introduction of a new trophic level (Section 9.3), incorporation of new links between subsystems (Section 9.4). A somewhat more general approach to the problem is the analysis of the probability that a community with a preassigned number of species, a fixed number of interspecific interactions and a certain level of intensities for them will have a stable structure. An increase in any of the enumerated community parameters may be regarded as an increase in system complexity, so that the explicit form of the relationship between probability of stability and these parameters could enable us to judge of the stability-complexity relation.

Notice that since *a priori* we have no reasons to think of interspecific interactions of one sign, say +, as of more complex ones than those of the sign —, the suggested approach in no way specifies the signs of interactions. If in considering different models we restrict ourselves to systems of ordinary differential equations, then similar considerations may be adduced concerning the particular form of the right-hand sides in the equations, i.e. the functional form of

interspecific interactions. As before, we shall assume only the existence of a non-trivial equilibrium in the system (with positive populations of all species), and that the model equations may be linearized at the equilibrium point. Then the problem of equilibrium stability is reduced to the analysis of eigenvalues for the community matrix (cf. Section 4.6) and the probability problem for stability of the structure may be stated in the following way.

Consider a community composed of n species, and suppose that in the absence of interspecific interactions of any kind all the species are stable. This means that all diagonal entries in matrix A are negative, i.e. all species feature self-regulation. For definiteness suppose that

$$a_{ii} = -1, \qquad i = 1, \ldots, n. \tag{9.27}$$

Define *connectance* of matrix A (or of the associated directed graph) as the fraction C of non-zero elements in A relative to the overall number of non-diagonal elements, $n(n-1)$ (or as the ratio o, actual links to topologically possible links in the graph). Clearlyf $0 \leqslant C \leqslant 1$, and the variable C may be regarded as the probability that an arbitrarily picked element a_{ij} turns out to be nonzero, or (in terms of community structure) that the j-species somehow affects the i-species.

Thus $a_{ij} = 0$ with probability $1 - C$ and $a_{ij} \neq 0$ with probability C, and if we believe that $a_{ij} > 0$ and $a_{ij} < 0$ with the same probability, then the magnitude of a_{ij} is to be chosen according to some probability law with zero mean and symmetric distribution density. An example is furnished by the normal distribution with zero mean and variance σ^2. The finite value of variance (which is the same for all a_{ij} to make it more simple) serves as an average measure for intensity of interspecific interactions.

Thus the community matrix A (together with the appropriate community structure) is randomly constructed in accordance with the rules:

$$\text{when } i = j, \qquad a_{ii} = -1, \qquad i = 1, \ldots, n;$$

$$\text{when } i \neq j \begin{cases} a_{ij} = 0 \text{ with probability } 1 - C, \\ a_{ij} \neq 0 \text{ with probability } C \text{ and chosen} \\ \text{from random distribution with zero} \\ \text{mean and variance } \sigma^2; \end{cases} \tag{9.28}$$

and we faced here a probability problem of determining

$$P(n, C, \sigma) = P\{\operatorname{Re} \lambda_i(A) < 0, \quad i = 1, \ldots, n\}, \tag{9.29}$$

i.e. the probability that the matrix chosen from the set of matrices with the foregoing features, will belong to a stable community.

It turns out that rather simple estimates of the probability $P(n, C, \sigma)$ hold for sufficiently large n: if

$$\sigma\sqrt{nC} < 1, \tag{9.30}$$

than $P(n, C, \sigma) \to 1$, and if

$$\sigma\sqrt{nC} > 1, \tag{9.31}$$

then $P(n, C, \sigma) \to 0$. This implies that as long as the condition (9.30) is met matrix A is almost always stable, and as soon as the increase in the number of species, n, or in the connectance, C, or in the interaction strength, σ (i.e. the increase in system complexity) brings about the condition (9.31), almost for sure A proves to be unstable. Thus, condition (9.30) specifies a threshold level of complexity, above which the system loses stability, and the transition to instability is very sharp.

Conditions (9.30) and (9.31) are derived for $n \gg 1$, however, numerous Monte Carlo computer studies indicate that they still work for moderate $n \sim 10$.

The conditions (9.30) and (9.31) lead us to the conclusion that two systems with the same number of species but different values for σ_1, σ_2 and C_1, C_2, most likely have similar stability character if

$$\sigma_1^2 C_1 \approx \sigma_2^2 C_2. \tag{9.32}$$

In other words, if within a stable structure C is large, i.e. each species interacts with many others, then they should do so rather weakly, and conversely, in structures with low connectances they should interact strongly enough. These conclusions often find support in practical ecology.

9.6. Criticism of previous method and alternative approaches

So definite a conclusion concerning stability in random structures, drawn in the preceding section, is to be expected in general, since it serves as an illustration for the general statistical regularity: systems assembled from a large number of identical stochastic elements are likely to have quite definite features. The scheme suggested for the construction of the community matrix is general enough on the one hand, since interactions are random both in their magnitude and sign, but on the other hand, it is too much restricted by condition (9.27), i.e. the assumption that all species regulate their own populations. Yet, it is not inconceivable that a part of species in the community, say, the autotrophic organisms in the absence of preying and competition for limiting resources, on the contrary, demonstrate positive feedback, i.e. $a_{ii} > 0$. The objections to total randomness in the constructing scheme used to structure the eco-

system, and accordingly to the resulting conclusion about the destabilizing effect of the increase in complexity, may essentially be reduced to the following two points:

1. Total randomness in the choice of a_{ij} neglects those links which are intrinsic in the system as the model of a biological community. For instance, if the species N_i serves as food for the species N_j, the uptake being characterized by the trophic function $V_{ij}(N_i)$, then, according to the arguments of Section 5.2, the increment in biomass of N_j cannot exceed $k_i V_{ij}(N_i)$, where $0 < k \leqslant 1$ is the efficiency of the prey biomass processing into the predator biomass. Therefore it follows that for a pair of species, i and j, the appropriate elements in matrix A are likely to be related by $|a_{ji}| \leqslant |a_{ij}|$. In the ecosystem with several trophic levels the signs of interactions between species in different levels are strictly determined and by no means random, and the fraction C of nonzero elements a_{ij} cannot already be randomly distributed over all the elements in A: at least some of a_{ij} which specify the interactions between species in different levels need be nonzero, since otherwise the notion of the trophic level itself becomes senseless. In this case only some elements a_{ij}, and not all of them as before, may be realized with probability C.

Allowance for restrictions of this kind in assembling the community matrix results in a wide variety of formal statements of problems and frequently yields the opposite result: with the increase in system complexity the probability of its stability grows too.

2. The random choice of matrix elements and the subsequent check of the condition $\operatorname{Re}\lambda(A) < 0$ presupposes tacitly that for any choice of elements the system has a non-trivial (positive) equilibrium $\mathbf{N}^*$. It is clear that actually this amounts to assuming that along with variations in a_{ij} reflecting the community structure, all the other system parameters are appropriately altered to provide existence of the equilibrium $\mathbf{N}^*$. For example, in Volterra systems (Chapters 4 and 6)

$$\frac{dN_i}{dt} = N_i\left(\varepsilon_i - \sum_{j=1}^{n} \gamma_{ij} N_j\right), \qquad i = 1, \ldots, n, \tag{9.33}$$

where the equilibrium $\mathbf{N}^*$ is found as a solution to the linear system of equations (4.16) with the interaction matrix and the right-hand side vector composed of environmental carrying capacities for each of the species, in these systems the change in matrix elements supposes an appropriate change in the right-hand sides, i.e. in environmental parameters. If we assume that the medium is constant, then variations in elements of the matrix (in their magnitude and sign), deforming the n-hedral angle of positive solutions (cf. Section 6.4), may bring the right-hand side vector out of this angle, i.e. the system will lack a positive equilibrium.

If, for instance, in (9.33) the populations $N_i(t)$ are expressed in fractions of the environmental capacity, i.e.

$$\gamma_{ii}/\varepsilon_i = 1, \qquad i = 1, \ldots, n,$$

then if all the remaining $\gamma_{ij} = \gamma$ are positive (entirely competitive community), the equilibrium values N_i^* will be

$$N_i^* = \frac{1}{1+\gamma(n-1)}, \qquad i = 1, \ldots, n, \tag{9.34}$$

but in the case that $\gamma_{ij} = -\gamma$ for all i, j (entirely symbiotic community)

$$N_i^* = \frac{1}{1-\gamma(n-1)}, \qquad i = 1, \ldots, n. \tag{9.35}$$

It is apparent from (9.34) and (9.35) that in the first case $N_i^* > 0$ for any number of species and interaction strength γ, whereas the second case calls for the condition $\gamma(n-1) < 1$ to be satisfied.

Considerations of this kind warranted the inclusion of only those cases in the random assemblage scheme of the community matrix A, which have positive equilibria $\mathbf{N}^*$ (some workers suggested to term these cases "feasible"). It turns out that the fraction of stable matrices on the set of feasible variants is much greater than on the set of all possible structures. Generally, the result is not quite evident, since the positiveness conditions of the equilibrium often prove to be sufficient for its stability, as is the case, for instance, with dissipative Volterra systems (cf. Section 4.3).

9.7. Connective stability

In the two foregoing sections it was shown that different schemes of random assemblage of the community structure lead just to the opposite conclusions about effects of complexity upon stability. There are even classes of matrices, however, which generally remain stable under variations in their elements and whose stability is preserved when the parameters n, C, σ are altered. In other words, the change in complexity for systems with such matrices in no way affects stability (if stability is only determined by the condition $\operatorname{Re}\lambda(A) < 0$).

An example of such a class of matrices is furnished by the sign-stable matrices (Section 4.6), for which the variations in elements that keep their sign structure, also preserve their stability. Thus, in this class the change in complexity via σ and n does not affect stability.

Another example is provided by the so-called matrices with *connective stability*, which are defined as follows. Let an $n \times n$ community matrix $\mathcal{A}$ with all diagonal elements negative be represented

in the form

$$\mathcal{A} = A - \operatorname{diag}\{\alpha_1, \ldots, \alpha_n\}, \tag{9.36}$$

where $A = \| a_{ij} \|$ and

$$\alpha_i > a_{ii} \geqslant 0, \qquad i = 1, \ldots, n. \tag{9.37}$$

Define the interconnection matrix as the matrix E with entries e_{ij} from the interval

$$0 \leqslant e_{ij} \leqslant 1, \qquad i, j = 1, \ldots, n; \tag{9.38}$$

if $e_{ij} \neq 0$ then the j-species affects the i-species. For each matrix $E = \| e_{ij} \|$ one may consider a matrix with elements

$$\begin{aligned} &a_{ii}e_{ii} - \alpha_i, && i = j, \\ &a_{ij}e_{ij}, && i \neq j, \end{aligned} \tag{9.39}$$

this implies that certain links of the original structure are weakened but all the diagonal elements remain negative for any values $e_{ii} \leqslant 1$.

Denote

$$\mathfrak{A} = \operatorname{diag}\{\alpha_1, \ldots, \alpha_n\}.$$

Matrix $\mathcal{A} = A - \mathfrak{A}$ is called connectively stable if for any interconnection matrix E the matrix

$$A * E - \mathfrak{A} \tag{9.40}$$

is stable, the symbol $*$ stands for the Adamar matrix product. In other words, for any values e_{ij} from (9.38) the matrix with elements (9.39) remains stable.

For communities, connective stability means that stability is preserved when the existing interspecific links are arbitrarily weakened (or even vanish). In the extreme case when $E = 0$ and the community disintegrates into n species in isolation, the maintenance of stability is assured by self-regulation in all species [the condition (9.37)].

It would be interesting to know what is the relation between the notions of connective and sign stability for matrices. Recall that the sign-stability criterion for matrices with negative diagonal elements is the absence of symbiotic and competitive interactions, as well as of closed loops with more than two elements in the associated signed directed graph (Theorem 1 from Section 4.6). Multiplication (in the sense of Adamar) by any interconnection matrix E implies, firstly, the change of the community matrix elements in magnitude, and secondly, the vanishing of certain a_{ij} (when the appropriate $e_{ij} = 0$), i.e. the erasing of the appropriate links in the directed graph. Variations in nonzero elements (which keep the sign) preserve stability by the sign-stability definition itself. And the erasure of

any combination of links $i \to j$ $(i \neq j)$ in the sign-stable graph can give rise neither to symbiotic or competitive interactions, nor to cycles with more than 2 members, i.e. again we get a sign-stable pattern. Thus, we have the relationship:

$$\boxed{\text{Sign-stability}} \overset{a_{ii}<0}{\Rightarrow} \boxed{\text{Connective stability}} \tag{9.41}$$

That this relationship is irreversible is readily seen from the example of a 2×2 matrix

$$\mathcal{A} = \begin{Vmatrix} -a & b \\ c & -d \end{Vmatrix}$$

with positive a, b, c and d, which satisfy the conditions of connective stability. Matrix $\mathcal{A}$ includes entries a_{12} and a_{21} of the same sign and therefore cannot be sign-stable.

We mention one sufficient condition of connective stability. If the matrix $\mathcal{A}$ has the absolute value of each diagonal element larger than the sum of moduli of all the other elements in the given column, then $\mathcal{A}$ is connectively stable. In fact, sufficiency of this "diagonal" property

$$|a_{jj} - \alpha_j| > \sum_{i \neq j}^{n} |a_{ij}|, \qquad j = 1, \ldots, n, \tag{9.42}$$

for stability of $\mathcal{A}$ follows, for instance, from the well-known localization criterion for eigenvalues—the Gershgorin cycles*, and then the same property also holds for an arbitrary interconnection matrix $E = \| e_{ij} \|$:

$$|a_{jj}e_{jj} - \alpha_j| \geqslant |a_{jj} - \alpha_j| > \sum_{i=j}^{n} |a_{ij}|, \qquad j = 1, \ldots, n,$$

i.e. matrix $A * E - \mathfrak{A}$ is also stable.

In ecological terms the condition (9.42) means that each of the community species to a greater degree affects itself (self-regulation), neither than all the other species.

Leaving now the theory of connectively stable matrices, we shall only remark that for this matrix class the decrease in connectance (in the fraction C of nonzero elements) and in the interaction strength does not disturb their stability and therefore gives no direct answer to the complexity-versus-stability problem.

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* Cf. Gantmacher F. R., *The Theory of Matrices*, Vols. 1 and 2. Chelsea Publishing Co., New York, 1960.

9.8. Conclusion

In the present chapter we have examined only a few of the possible approaches to the mathematical analysis of the complexity-versus-stability problem. While changing due to variations in numbers of species and trophic levels, in the degree of structural connectance and interaction strength, the stability implied only asymptotic stability of equilibrium in a linear approximation. But even under these constraints the examples considered show that higher complexity in models of ecosystems may (a) reduce the probability of stability, (b) increase this probability, and (c) in no way affect stability. The interpretation of results from other chapters also supports this ambiguity of conclusions about the effect of complexity on stability. For instance, the stability conditions in models of competitive communities (Chapter 6) impose quite definite restrictions on the ecological niche overlap, so that the increase in the number of species over the same resource spectrum results in instability. The amalgamation of several subsystems into one (migration models of Chapter 8) may have stabilizing as well as destabilizing effects.

In this aspect we could comment along similar lines on practically all the results of stability analysis in dynamic models of biological communities. But using the words of a well-known physicist, we shall not "obscure further this already well confused subject"*. The only obvious conclusion is that within the framework of mathematical models there is no use looking for a *unique* relation between complexity and stability, that in particular cases is determined by peculiarities of structures under consideration and the specific character of mathematical formulations.

9.9. Notes and bibliography

To 9.1. A brief survey of arguments in favor of both viewpoints on the problem of relation between complexity and stability, as well as literature references may be found in:

May R. M., *Stability and complexity in model ecosystems*, Princeton Univ. Press, Princeton, Ch. 3, 1973;

Maynard Smith J., *Models in ecology*, Cambridge Univ. Press, Cambridge, Ch. 7, 1974.

Some attempts to give a formal definition of the complexity measure for a trophic web were undertaken for a two-level predator-prey system:

Casty J., "Connectivity, complexity and resilience in complex ecosystems," In: "*IFAC—Symposium on Control Mechanisms in Bio- and Ecosystems*," September 1977, Leipzig, 1977, V. 1, pp. 34-46.

To 9.2. The properties of eigenvalues for matrix (9.3) as well as of system

* Cited from the book: Kats M., *Some probability problems of physics and mathematics*, Nauka, Moscow, 1967, p. 176 (in Russian).

(9.8)-(9.9) are discussed in the works:

May R. M., "Stability in model ecosystems," *Quantifying Ecology*, 6, pp. 18-56, 1971;

May R. M., "Stability in multispecies community models," *Math. Biosci.*, 12, 1/2, pp. 59-79, 1971,

the second one includes more mathematical technicalities and also examples of model trajectories for system (9.1) with $n = 2$ for a neutrally stable and unstable equilibrium.

To 9.3. The reasoning in this section follows Chapter 3 of the above-cited monograph by R. May.

There are also references where one may find arguments in favor of different alternatives (I-IV) of the relationship between stability in one trophic level and stability of a two-level system on the whole.

To 9.4. The results presented here were derived in the work:

Logofet D. O., "Study of a system of n predator-prey pairs linked by competition," *Dokl. Acad. Nauk. SSSR*, 224, 3, pp. 529-531, 1975 (in Russian).

To 9.5. The idea of a random assemblage of a community matrix for the study of the complexity-versus-stability problem was first developed in the work:

May R. M., "Will a large complex system be stable?," *Nature*, 238, 5364, pp. 413-414, 1972,

where the estimates (9.30) and (9.31) were also obtained. Results of Monte-Carlo modeling and of the stability analysis of community matrices confirming these estimates may be found in:

Gardner M. R., Ashby W. R., "Connectedness of large dynamical (cybernetic) systems: critical values for stability," *Nature*, 228, 5273, p. 784, 1970;

Daniels J., Mackay A. L., "The stability of connected linear systems," *Nature*, 251, 5468, pp. 49-50, 1974;

Saunders P. T., Bazin M. J., "Stability of complex ecosystems," *Nature*, 256, 5513, pp. 120-121, 1975;

Pimm S. L., Lawton J. H., "Number of trophic levels in ecological communities," *Nature*, 268, 5618, pp. 329-331, 1977.

To 9.6. The conclusion that more complex structures are stable with a greater probability, was drawn from the analysis of random structures under different restrictions:

Makridakis S., Faucheux C., "Stability properties of general systems," In: "*Gen. Syst*," Yearbook Soc. Gen. Syst. Res. Washington, V. 18, pp. 3-12, 1973;

Webber M. I., "Food web linkage complexity and stability in a model ecosystem," In: "*Ecological Stability*," Eds. M. B. Usher, M. H. Williamson. L., 1974;

De Angelis D. L., "Stability and connectance in food web models," *Ecology*, 56, 1, pp. 238-243, 1975.

The concept of feasible systems was suggested in:

Roberts A., "The stability of a feasible random ecosystem," *Nature*, 251, 5476, pp. 607-608, 1974;

MacDonald N., "The stability of a feasible random ecosystem," *Math. Biosci.*, 27, 1/2, pp. 141-143, 1975.

To 9.7. In a somewhat different but equivalent form the notion of connective stability was suggested in the papers:

Šiljak D. D., "Connective stability of complex ecosystems," *Nature*, 249, 5454, p. 280, 1974;

Šiljak D. D., "When is a complex system stable?" *Math. Biosci.*, 25, 1/2, pp. 25-50, 1975.

In the second one a series of theorems about stability and instability of equilibrium is proved for systems of a more general form than the linear one, namely for such systems where elements of A are bounded functions of time and state variables and the diagonal property (9.42) is satisfied. It should be noted that a lot of these results found analogies in systems of stochastic differential equations:

Ladde G. S., Šiljak D. D., "Stochastic stability and instability of model ecosystems," In: "*Proc. IFAC 6th World Congr.*," Boston-Cambridge, 1975, Pittsburg, 1975, p. 3, pp. 55.4/1-55.4/7.

POSTSCRIPT

In our book we attempted to give a more or less systematic picture of the state-of-the-art in stability problems of biological communities. Interestingly, that purely ecological problems give rise to new mathematical formulations, and their investigation in turn results in new questions to practical specialists involved in ecological studies.

Recently, the opinions are more and more often voiced that the traditional mathematical definitions of stability are clearly insufficient to account for the "intuitively ecological" notion of stability. For example, an ecosystem or a community may have several equilibrium states, each with its own domain of attraction; however, the behavior in the stable states may be radically different. In particular, because of stochastic effects or human activity one or several species may die out and accordingly, the appropriate trophic links will vanish. For this reason, some ecologists, C. Holling* for example, suggest to analyze the feature of "resilience" together with stability of a community.

The formalization of the resilience notion poses a class of interesting mathematical problems, concerned with qualitative analysis of the system's phase space topology.

Further, each system has its own hierarchy of characteristic times, and the existence time of the entire system usually coincides with the life span of the species (or the trophic level) which has the largest characteristic time. If we incorporate the time hierarchy into a model of such a system and test this model for stability, it is quite likely that the system as a whole will have no stability although separate blocks (or levels) will be stable (in "their own" time). These speculations underlie the concept of "hierarchical stability"**, whose

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* Holling C. S., Resilience and stability of ecological systems, *Ann. Rev. Ecol. and Syst.*, 4, 1-23, 1973.

** Svirezhev Yu. M., "Hierarchical stability in biological communities", In: *Mathematical modelling of marine ecosystems*, Naukova Dumka, Kiev, pp. 44-46, 1974 (in Russian).

essence consists in the following. Any ecosystem, as a rule, is unstable in the classical sense. However, this instability shows up during long periods of time exceeding the time of the existence of the ecosystem. The instability of an individual block (level) is redeemed by the block arranged higher in the hierarchy. Usually, a natural hierarchy of characteristic times is employed that generates a structural hierarchy in which the behavior of the higher block determines the general behavior of the lower block, the behavior of the highest block being determined, in turn, by exogeneous factors. For example, in terrestrial ecosystems, the plant biomass evolution depends mainly upon periodical changes in environmental conditions (light, temperature, humidity, etc.). But the state of this highest block determines essentially the dynamics of insects, fungi, microorganisms, etc., i.e. the dynamics of the next trophic levels.

Finally, concluding our book, once again we would like to stress that the stability problem in mathematical ecology by no means may be classed with solved or nearly solved problems. Perhaps, we can say that it is only in the stage of formation. We are still too much restricted by the burden of ideas and concepts from the classic stability theory, and therefore any new ideas, concepts, methods may be only welcomed.

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